THE LEPTOCERATOIDINAE: SMALL HETEROMORPH AMMONITES FROM THE BARREMIAN

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† deceased 2 December 1993

ABSTRACT. The Barremian Leptoceratoidinae, a subfamily of small-sized heteromorph ammonites, are revised. Despite considerable differences in the mode of uncoiling, Leptoceratoidinae are considered to represent a monophyletic unit, defined by their small size, simplified suture-lines and ubiquitous Barremian age. Three evolutionary lines are recognized exhibiting parallel trends of size increase: (1) *Karsteniceras* with criocone uncoiling and a planispiral to trochospiral initial coil; (2) *Hamulinites* with an ancylocone type of uncoiling and a small planispiral initial coil; and (3) a line compromising *Eoheteroceras* gen. nov. with ancylocone uncoiling and a large trochospiral initial coil, as well as *Manoloviceras* gen. nov. with only one slightly curved arm and a large trochospiral initial coil. It is inferred that these evolutionary lines originated in *Veveysiceras* gen. nov. with hamitid-like uncoiling. *Velezíceras*, with a straight to gently curved shell, is tentatively included in the Leptoceratoidinae, but cannot yet be assigned to one of the three lines defined above. The following new species are described: *Karsteniceras ibericum*, *K. beyrichoide*, *K. hoheneggeri*, *K. trinidadense* and *E. silesiacum*, the type species of *Eoheteroceras* gen. nov. The origin of leptoceratoids remains obscure; they are not closely related to the Berriasian to Valanginian true leptoceratids. Presumably, *Eoheteroceras* gave rise to the large-sized *Heteroceras*. Due to the simplified suture-line formula *ELUI* and the type of uncoiling, the Leptoceratoidinae are included in the Ancyloceratidae. Their evolutionary centre was the southern (Tethyan) margin of the European Plate. From this area, Leptoceratoidinae migrated into the central North Atlantic and even the western Pacific. While Leptoceratoidinae presumably had a vagrant epibenthic mode of life, their dispersal was most probably achieved during their nearshore juvenile stage by the North Equatorial Current.

WHEN Uhlig (1883) created *Leptoceras* as a subgenus of *Crioceratites*, a long history of misinterpretation, misconception and misdating began. Uhlig was convinced that these small-sized criocones were a well defined monophyletic group of Barremian age. More than sixty years later, Thieuloy (1966) demonstrated convincingly that Uhlig lumped at least two different but homoeomorphic groups together, one of Berriasian to Valanginian, the other of Barremian age. Unfortunately, Uhlig's type species, *Leptoceras brunneri*, belongs to the earlier stock. Both groups are phylogenetically separate, they exhibit different suture patterns, and no transitional forms of Hauterivian age are found. Since, however, the Barremian stock comprises criocones, ancylocones and hamiticones with planispiral or trochospiral initial coils, the question arises whether all these forms are really monophyletic or micromorphic descendants of these different groups. This was the starting point of the present revision. Difficulties were encountered because some of the type specimens are lost, and others too poorly preserved to allow reliable identification and interpretation. Therefore, recollection of material became necessary to obtain well-preserved specimens from well-dated sections.

HISTORICAL REVIEW

The extremely difficult and controversial interpretation of Leptoceratoidinae can be evaluated only by reviewing the history of research. The first scanty representatives were described by d'Orbigny (1850) from France, by Karsten (1858) from Colombia, and by Ooster (1860) from Switzerland, as small *Crioceratites* or *Ancyloceras*. Uhlig (1883) realized the peculiarity of these forms when he

[Palaeontology, Vol. 37, Part 1, 1994, pp. 203–239, 4 pls.]

studied a relatively rich fauna from the Barremian of Silesia. Based on the simplified suture-lines, he considered the ancylocone and criocone 'microconchs' to represent a new subgenus *Leptoceras* of *Crioceratites*. Unfortunately, no type species was designated. *Leptoceras* was accepted by Sayn (1891) for small fragments of criocones (*L. cirtae*) first mentioned by Conquand (1880) from the Barremian of Algeria. Nicklès (1894) described a small Barremian hamulinicone from the Subbetic of Spain which was designated the type of the new genus *Hamulinites* by Paquier (1901). Sarasin and Schöndelmayer (1902), when redescribing Lower Cretaceous ammonites from Switzerland, accepted some of Ooster's species but considered them to be juvenile fragments of well-known large-sized genera.

New species of *Leptoceras* were described by Yabe *et al.* (1926) from Japan, and by Stahlecker (1935) from the Barremian of Maio, Cape Verde Islands. The *Essai de genera* published by Roman (1938) became the source of serious problems for the next few decades: Roman proposed *Ancyloceras brunneri* Ooster, the first listed species of Uhlig, as the type species, but figured erroneously *Leptoceras pumilum* Uhlig under the name *L. parvulum* Uhlig (Roman 1938, pl. 35, figs 335–336). Much later, Thieuloy (1966) realized that, beginning with Ooster (1860), two similar but distinct groups of 'microconchs' had been included in *Leptoceras*: (1) a Berriasian group centred around *L. brunneri* (Ooster); and (2) a Barremian group centred around *L. pumilum* Uhlig.

Meanwhile, Royo y Gómez (1945) proposed the new genus *Karsteniceras* for *Ancyloceras beyrichi* Karsten, 1858, and also created the similar genus *Orbignyceras* with *O. veleziense* as type species. Both genera were first described from the Barremian of Colombia.

Wright (1957) renamed the pre-occupied *Orbignyceras* as *Veleziceras*, and included it together with *Karsteniceras* in his subfamily Crioceratitinae, while *Leptoceras*, with *L. pumilum* Uhlig as type species, was considered to belong to Ancyloceratinae. This obvious misinterpretation of the criocone *L. pumilum* may be due to Roman's previous mistake. Luppov and Drushtchic (1958) followed the same interpretation.

Manolov (1962) created the new genus *Eoleptoceras* for the ancylocone species *L. parvulum* Uhlig, with two more new subgenera, *Tzankoviceras* and *Wrighticeras*. These and the criocones *Leptoceras*, *Karsteniceras* and *Veleziceras* were all considered to be of Barremian age and to form the new crioceratid subfamily Leptoceratinae.

Wiedmann (1963) drew attention to the fact that *Eoleptoceras* and *Tzankoviceras* Manolov were objective synonyms, and that they were subjective synonyms of *Hamulinites* Paquier and *Wrightites* Manolov. He also described the suture ontogeny of *Hamulinites*.

When Thieuloy (1966) separated the Berriasian stock from that of the Barremian, he created the new genus *Leptoceratoides* for the Barremian forms around *Leptoceras pumilum* Uhlig, and proposed, accordingly, to restrict Leptoceratinae to the early stock and created Leptoceratoidinae for the Barremian forms. *Leptoceras* Uhlig (type species *L. brunneri*), however, was restricted to the Berriasian, and included in the Protancyloceratinae Breistroffer and consequently, in the Bochianitidae Spath. Nikolov (1966) described a new genus *Protoleptoceras*, based on *P. jelevi* Nikolov, from the Berriasian of Bulgaria, which became a synonym of *Leptoceras*.

Breskovski (1966), Dimitrova (1967), and Nagy (1967) added further material from Bulgaria and Hungary, following Wright's and Manolov's systematic concepts. Dimitrova included, moreover, the Berriasian *Protoleptoceras* Nikolov in 'Leptoceratinae' *sensu* Manolov. In 1968, Etayo Serna revised the Colombian *Karsteniceras beyrichi* (Karsten) and placed *Karsteniceras* in the Leptoceratoidinae Thieuloy.

In 1970, Dimitrova made an attempt to classify Lower Cretaceous heteromorphs based on their shape and adult suture-lines. The result is, however, hard to understand since the Berriasian *Protoleptoceras* was lumped with the Barremian *Karsteniceras* in the Scaphitaceae which originated in the Albian. All the remaining genera (*Leptoceras*, *Tzankoviceras*, *Eoleptoceras*, *Hamulinites*) were considered Barremian, and again included in the Leptoceratidae and these in the Protancyloceratacеae.

Vašíček (1972) followed Thieuloy's classification when describing new discoveries of leptoceratids from the Moravo-Silesian Barremian. Wiedmann (1973) also followed Thieuloy, at least in

including the Berriasian *Leptoceras* in Protancyloceratinae; the Barremian microconchs were reduced to two genera, *Karsteniceras* Royo y Gómez (= *Veleziceras*, = *Leptoceratoides*) for the criocones, and *Hanulinites* Paquier (= *Eoleptoceras*, = *Tzankoviceras*, = *Wrightites*) for the ancylocones, and these two genera were included in the Ancyloceratinae Meek. Myczyński (1977) and Myczyński and Triff (1986) followed this interpretation when describing species of *Karsteniceras* and *Hanulinites* from the Barremian of Cuba. Roumanian leptoceratoids were described by Avram (1976) who used Leptoceratidae Manolov and again included *Karsteniceras* in the Scaphitidae (*sensu* Dimitrova 1970).

New species were recorded and described from the Southern Alps (Rieber 1977), northern Calcareous Alps (Darga and Weidich 1986; Immel 1987) and, again, from Roumania (Avram and Kusko 1984). Immel (1987) preferred to attribute *Karsteniceras* to the Crioceratitinae, while Wright (1981) synonymized Leptoceratoidinae with the Helicancylinae. This idea was shared by González-Arreola and Carillo-Martínez (1987) when they published on Mexican *Karsteniceras*. Finally, Matsukawa (1987) followed Wiedmann's classification in his careful study of the early ontogeny of a new Japanese *Karsteniceras*.

Despite the fact that the rather divergent views of the 1960s have become more focused during the last decade, the systematics of this group is still unsatisfactory and needs revision.

SYSTEMATIC PALAEONTOLOGY

Material. The material studied is deposited in the following collections: BSM, Bayerische Staatssammlung für Paläontologie und Historische Geologie, München; GBAW, Geologische Bundesanstalt, Wien; GPIT, Geologisch-Paläontologisches Institut, Tübingen; MHNG, Musée d'Histoire Naturelle, Genève; MHNP, Musée d'Histoire Naturelle, Paris; NMB, Naturhistorisches Museum, Bern; OSM, Ostrava-Museum, Ostrava; SNM, Slovak National Museum, Bratislava; USNM, National Museum of Natural History, Smithsonian Institution, Washington; VŠB, Vysoká Škola Báňská, Ostrava.

Additional unstudied type material is kept in the following collections: HNM, Hungarian National Museum, Budapest; IGPH, Instituto Geológico, La Habana; IGPS, Institute for Geology and Palaeontology, Sendai; MPMS-R, Museo paleontológico 'Mario Sanchez Roig', La Habana; NSMT, National Science Museum, Tokyo; PIMUZ, Paläontologisches Institut und Museum, Universität Zürich; SGM, State Geological Museum, University of Sofia; SGNB, Servicio Geológico Nacional, Bogota.

Morphological abbreviations. The following abbreviations are used: D, diameter; H, whorl height; R, ribs per whorl (of half whorl R/2); U, umbilical diameter; W, whorl width. Suture symbols, applied according to Wedekind's (1916) suture terminology (see Kullmann and Wiedmann 1970): *E*, external lobe; *L*, lateral lobe; *U*, umbilical lobe; *I*, internal lobe.

Superfamily ANCYLOCERATACEAE Gill, 1871
Family ANCYLOCERATIDAE Gill, 1871
Subfamily LEPTOCERATOIDINAE Thieuloy, 1966

Remarks. Leptoceratoidinae are interpreted to include micromorph heteromorphs with elliptical, criocone, ancylocone or slightly curved types of coiling, sometimes with a tendency towards torsion, especially of the initial coil. The suture-line has elements *E*, *L*, *U*, *I*, poorly incised.

The following genera are included in the Leptoceratoidinae: *Veveysiceras* gen. nov., *Karsteniceras* Royo y Gómez, *Hanulinites* Paquier, *Veleziceras* Wright, *Eoheteroceras* gen. nov., and *Manoloviceras* gen. nov.

Most authors refer to Wright (1957) when considering leptoceratids in their entirety to be members of the Ancyloceratidae. However, Wright split the Colombian genera *Karsteniceras* and *Veleziceras* from *Leptoceras*, and included the two former genera in the Crioceratitinae. Like Wright, Manolov (1962) considered *Leptoceras* to be exclusively Barremian when he proposed Leptoceratinae as a separate subfamily of Ancyloceratidae for the bulk of leptoceratids. When Thieuloy (1966) corrected the scope and stratigraphical position of *Leptoceras*, giving *L. bruneri* as the type species and citing a Berriasian age, he proposed the new genus *Leptoceratoides*, as well

as Leptoceratoidinae, for the Barremian criocones centred around *L. pumilum*. Wiedmann (1973) revived the old genera *Karsteniceras* and *Hamulinites* to include all criocone and ancylocone Barremian micromorphs which were now both included in the Ancyloceratinae. Most successive authors followed this interpretation, except Immel (1987) who referred *Karsteniceras* to the Crioceratitinae, and Gonzáles-Arreola and Carrillo-Martínez (1987) who referred this genus to the Helicancylinae Hyatt, 1894.

As a result of the present investigation, the Barremian leptoceratids are considered to represent a micromorphic stock which separated in the late Hauterivian to early Barremian, presumably from the main stock of the Crioceratitinae (Text-fig. 7). Three divergent evolutionary lines may have originated from the basal Lower Barremian *Veveysiceras*, the ancestor of which is still unknown. It has to be noted that there is, however, no connection with the Tithonian/Berriasian Protancyloceratinae Breistroffer.

Distribution. Barremian, mainly Lower Barremian. Southern, eastern and central Europe, Cape Verde Islands, Central and South America, Japan. The origin of the subfamily (in late Hauterivian time?) remains obscure. No certain representatives from the Lower Aptian are known.

Genus VEVEYSICERAS gen. nov.

Type species. Ancyloceras escheri Ooster, 1860.

Diagnosis. Elliptically coiled, in three arms. After the first planispirally-coiled whorl passing into a hook, similar to *Hamulinites*. This is followed by two more elliptical half-whorls. Smooth at first, the shell on the hooks is covered by fine, dense and simple ribs directed radiate or prorsiradiate on the lateral side. On the last arm a few weak constrictions are added. Suture-line *E, L, U, I* with simplified elements.

Remarks. Coiling is more irregular than in the other genera of the subfamily. Starting with a hook which is followed by an elliptical whorl, *Veveysiceras* is characterized by more arms than are present in *Hamulinites* and *Karsteniceras*. Moreover the sculpture is much finer.

Distribution. Lower Barremian of Switzerland, southern France and the Western Carpathians of Slovakia.

Veveysiceras escheri (Ooster, 1860)

Plate 1, figures 1–3; Text-figure 1A

1860 *Ancyloceras Escheri* Ooster, p. 29 [*partim*], pl. 37, figs 1, 7–9, ?6; *non* fig. 2 [= *Hamulinites fragilis* (Uhlig)]; *non* figs 3–4 [= *Karsteniceras pumilum* (Uhlig)]; *non* fig. 5 [= *Crioceratites*? sp.].

EXPLANATION OF PLATE 1

Figs 1–3. *Veveysiceras escheri* (Ooster). 1, NMB 5721, holotype; Hauterivian/Barremian boundary; Veveyse, Vaud, Switzerland; ×2. 2, GPIT 1719/1; Lower Barremian; Castellane, Haute Provence, France; ×1·5. 3, SNM Z 21124; Lower Barremian; Zabukovinské quarry near Lietavska Lúčka, Central Western Carpathian, Slovakia; ×1.

Figs 4–5. *Karsteniceras ibericum* sp. nov. GPIT 1719/2, holotype; Upper Barremian; Barranco de las Higueras, Sierra Mediana, Subbetic of Alicante, Spain; lateral and ventral views; ×1·5.

Figs 6–8. *Karsteniceras beyrichoide* sp. nov.; Upper? Barremian; Nýdek, Outer Carpathians, Czech Republic. 6, GBAW 3902, ×1. 7–8, GBAW 3911, holotype; lateral and oblique view, showing the slight torsion; ×1.

Fig. 9. *Karsteniceras pumilum* (Uhlig). BSM AS III 96, lectotype; Lower Barremian; Straconka, Outer Carpathians, Poland; ×1.

Arrows indicate position of last suture-line.

VAŠÍČEK and WIEDMANN, *Veveysiceras*, *Karsteniceras*

1902 *Crioceras* (*Leptoceras*) *Escheri* Ooster; Sarasin and Schöndelmayer, p. 148 [*partim*], pl. 19, fig. 6; non fig. 4 [= *Hamulinites fragilis*]; non fig. 5 [= *Crioceratites*? sp.].

Lectotype (designated herein). NMB 5721 (coll. Ooster); Lower(?) Barremian; Veveyse near Châtel St Denis, Switzerland; here refigured as Plate 1, figure 1, originally figured by Ooster (1860, pl. 37, fig. 1).

Other material. GPIT 1719/14 from the Lower Barremian of Castellane, France; SNM Z-21124 and unregistered fragments from Križna Nappe, Slovakia.

Diagnosis. As for genus.

Description. To the generic description can be added that in the holotype the first hook (= *Hamulinites*) measures 20 mm in length, while the maximum diameter ranges between 37 and 40 mm; the small diameter of the ellipsoid is 30 mm; it measures 33 mm in a Carpathian and 19 mm in a French specimen. Maximum whorl height of the holotype is 8 mm. This means that there is some variation in shell size and in elliptical to subcircular coiling. The ornamentation consists of fine to very fine and densely spaced radiate ribs on the phragmocone and more pronounced ribs on the living chamber. The suture-line (Text-fig. 1A) is only partly visible, *L* and *U* are moderately incised and tripartite, the saddles asymmetric bipartite.

Occurrence. The type material is from the Hauterivian/Barremian boundary at Veveyse near Châtel St Denis, External Prealps, Switzerland. New specimens were collected from the Lower Barremian of Castellane, Vocontian Trough, France, and the basal Barremian of Lietavská Lúčka, Trstie (Krížna Nappe), Central Western Carpathians, Slovakia.

Genus KARSTENICERAS Royo y Gómez, 1945

[= *Leptoceratoides* Thieuloy, 1966, p. 289].

Type species. Ancyloceras beyrichi Karsten, 1858.

Revised diagnosis. Small criocones with planispiral to indistinctly trochospiral initial coil, thereafter loosely coiled. Initial coil smooth, then with simple ribs increasing in strength. Ribs generally crossing venter; in some species, rib-weakening on the siphonal line leads to the development of a ventral furrow. The later forms may have marginal tubercles or at least swellings on both sides of the furrow either on each rib or periodically. Periodic constrictions may be present or not. Suture-lines with simplified elements *E, L, U, I.*

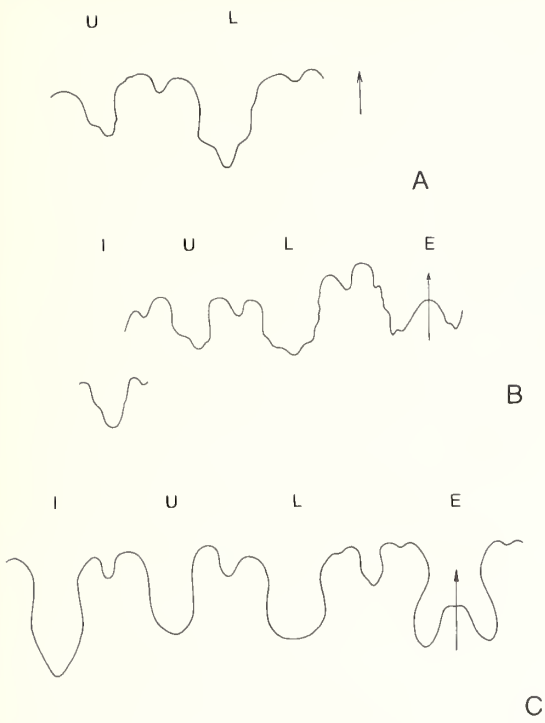
Remarks. Leptoceratoides is a synonym of *Karsteniceras*. In contrast to the opinion of Matsukawa (1987), we regard the existence of constrictions as insignificant for generic separation in karsteniceratids.

Karsteniceras differs from most other members of this subfamily in its criocone coiling. *Veveysiceras* gen. nov. with its elliptical coiling is closest, but differs in its fine and dense ribbing. Small-sized or internal whorls of crioceratitids can easily be mistaken for leptoceratids but have much more complicated lobes and saddles from the very beginning. Moreover, the main ribs of crioceratitids often carry from one to three tubercles.

The following species are now included in *Karsteniceras*: *K. asiaticum* (Yabe and Shimizu), *K. balernaense* Rieber, *K. beyrichi* (Karsten), *K. beyrichoide* sp. nov., *K.? filicostatum* (Stahlecker), *K.? heeri* (Ooster), *K. hoheneggeri* sp. nov., *K. ibericum* sp. nov., *K. obatai* Matsukawa, *K. polieri* Myszyński, *K. pumilium* (Uhlig), *K. subtile* (Uhlig), and *K. trinidadense* sp. nov.

Species can be separated by differences in mode of ribbing and ventral sculpture. Ooster's species '*Ancyloceras*' *brunneri* and '*Ancyloceras*' *studeri* are true Berriasian to Lower Valanginian *Leptoceras*, whereas '*Ancyloceras*' *escheri* Ooster is the type species of *Veveysiceras* gen. nov.

Uhlig's species *L. assimile*, *L. fragile* and *L. parvulum* are now transferred to *Hamulinites*. Of d'Orbigny's (1842) small-sized criocones, '*Crioceras*' *puzosianum* is unidentifiable. No similar



TEXT-FIG. 1. Leptoceratoid suture-lines. A, fragmentary suture-line of *Veveysiceras escheri* (Ooster) at H = 2 mm; NMB 5721. B, *Karsteniceras beyrichi* (Karsten), external part at H = 5·2 mm, internal lobe at H = 4 mm; USNM 18609. C, *K. ibericum* sp. nov., complete suture-line of holotype, GPIT 1719/2, at H = 3·2 mm.

specimen can be located in d'Orbigny's collection (Sarkar 1955, p. 160, and personal enquiries); nevertheless, Sarkar (1955) cited this species as characteristic of his genus *Spathicrioceras*. '*Crioceras*' *cristatum* d'Orbigny differs from *Karsteniceras* in its more complicated suture-line. It was also cited by Sarkar (1954) as the type species of another new genus, *Escragnolleites*, which was later referred to *Imerites* Roukhadze by Wright (1957).

The position of '*Ancyloceras*' *pugnairei* Astier, 1851 remains uncertain due to the lack of similar specimens and its unknown suture-line. '*Toxoceras*' *cirtae*, described by Coquand (1880) from the Barremian of Djebel Ouach, was later assigned to *Leptoceras* (Sayn 1891; Kilian 1910). A syntype from the same locality shows that *T. cirtae* is similar to *Karsteniceras* but has a more complicated suture-line.

Distribution. Karsteniceras is a Barremian genus. It is widespread at the northern margin of the European Tethys (Text-fig. 9), and ranges into the Caribbean and the Japanese Islands.

Karsteniceras beyrichi (Karsten, 1858)

Plate 2, figures 1–2; Text-figure 1B

1858 *Ancyloceras Beyrichii* Karsten, p. 103, pl. 1, fig. 4*a–d*.

non 1945 *Karsteniceras beyrichi* (Karsten); Royo y Gómez, p. 461, pl. 71, fig. 1*a–c*, text-fig. 1 [= *Karsteniceras ibericum* sp. nov.].

?1954 *Leptoceras* cf. *L. beyrichii* (Karsten); Imlay, p. 664, pl. 74, figs 23–24.

non 1966 *Leptoceras beyrichi* (Karsten); Breskovski, p. 79, pl. 6, fig. 1 [? = *Karsteniceras heheneggeri* sp. nov.].

non 1967 *Karsteniceras beyrichi* (Karsten); Dimitrova, p. 38, pl. 12, fig. 6 [? = *Karsteniceras heheneggeri* sp. nov.].

1968 *Karsteniceras beyrichi* (Karsten); Etayo Serna, p. 54 (*partim*), pl. 1, figs 5, 7; non figs 1–3, text-fig. 1 [= *Karsteniceras ibericum* sp. nov.].
non 1986 *Karsteniceras beyrichi* (Karsten); Darga and Weidich, pl. 3, fig. 3.
?1987 *Karsteniceras beyrichi* (Karsten); Gonzáles-Arreola and Carillo-Martínez, p. 174, fig. 3.
non 1987 *Karsteniceras beyrichi* (Karsten); Immel, p. 118, pl. 12, fig. 6.

Holotype. The specimen, probably lost, figured by Karsten (1858, pl. 1, fig. 4); Barremian; Vélez, Colombia.

Material. One nearly complete specimen, USNM 18609; from Vélez-Chipatá, Colombia.

Revised diagnosis. Criocone with oval to round whorl section. At the beginning ribs are uniform, simple and of equal width as intervals. After a diameter of 20 mm, one or two stronger ribs alternate with bundles of 1–4 less pronounced ribs. Initially all ribs with marginal tubercles, and crossing venter. Sometimes with a ventral depression. In some specimens, looping of strong ribs between the tubercles. Suture poorly incised; *E* with broad median saddle, broad *L*, narrow and asymmetric *U*; saddles asymmetrically bipartite.

Measurements. At D = 22 mm, the following measurements were made on specimen USNM 18603: H = 6 mm (0·27), W = 6 mm (0·27), U = 8·5 mm (0·39). At D_{max} = 24 mm, 35 R/2.

Remarks. From the Colombian specimens previously published (Karsten 1858; Etayo Serna 1968) and described in this paper, we can conclude that *K. beyrichi* has a highly variable ribbing. This is less pronounced in the holotype which is probably lost. The holotype shows a broad and flattened venter, but no furrow between the indistinct ventrolateral tubercles, as in the specimen figured here in Plate 2, figure 2. The specimens figured by Royo y Gómez (1945) and some of those of Etayo Serna (1968) have a distinct ventral furrow and are considered to belong to *K. ibericum* sp. nov.

Karsteniceras beyrichioide sp. nov. can only be separated in its adult stage during which the ribbing remains uniform. The other species of *Karsteniceras* are easily distinguishable by the uniformity of ribs, or by the lack of tubercles which exist in some species only for a very short period.

The specimens referred to *K. beyrichi* by Imlay (1954) and Gonzáles-Arreola and Carrillo-Martínez (1987) are juveniles or are too fragmentary to be included with certainty in this species.

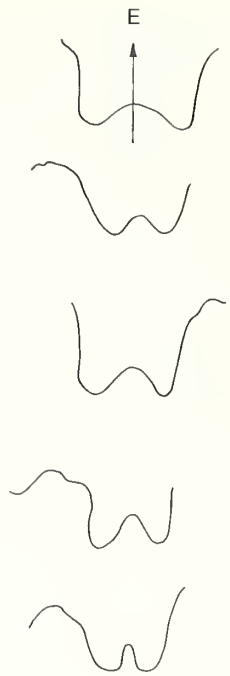
The specimens figured by Darga and Weidich (1986) and Immel (1987) from the Austroalpine Lower Barremian are different from *K. beyrichi* and even the bulk of *Karsteniceras* species in the presence of marginal spines where some of the ribs amalgamate. Moreover, their suture-lines are unknown. Due to these reasons, both specimens are excluded from the karsteniceratids.

Occurrence. Karsteniceras beyrichi is known in the Lower to Upper Barremian transition from Vélez-Chipatá, Colombia, and questionably from the Santuario Formation of Maravillas, Mexico, and from Tompire Bay, Trinidad.

EXPLANATION OF PLATE 2

Figs 1–2. *Karsteniceras beyrichi* (Karsten). USNM 18609; Lower/Upper Barremian boundary; Vélez – Chipatá road, Santander Department, Colombia; lateral and ventral views; ×2.
Figs 3–4. *Karsteniceras pumilum* (Uhlig). 3, BSM AS III 98; Lower Barremian; Straconka, Outer Carpathians, Poland; ×2. 4, NMB 5725; Lower Barremian; Veveyse, Vaud, Switzerland; ×1.
Figs 5–8. *Karsteniceras subtile* (Uhlig). 5, GBAW 3949, lectotype; Lower Barremian; Skalice, Outer Carpathians, Czech Republic; ×2. 6, GBAW 3901; Lower Barremian; Nýdek, Outer Carpathians, Czech Republic; ×2. 7, GBAW 3948; Lower Barremian; Skalice, Outer Carpathians, Czech Republic; ×2. 8, GPIT 1719/3; Lower Barremian; Sierra del Valle, Subbetic of Cadiz, Spain; ×2.
Fig. 9. *Karsteniceras hoheneggeri* sp. nov. BSM AS III 179, holotype; Upper? Barremian; Malenovice, Outer Carpathians, Czech Republic; ×1.

VAŠÍČEK and WIEDMANN, *Karsteniceras*



TEXT-FIG. 2. *Karsteniceras ibericum* sp. nov. Variability in *E* at H between 7 and 7·5 mm; GPIT 1719/11.

Karsteniceras ibericum sp. nov.

Plate 1, figures 4–5; Text-figures 1c, 2

1945 *Karsteniceras beyrichi* (Karsten); Royo y Gómez, p. 461, pl. 71, fig. 1; text-fig. 1.
1968 *Karsteniceras beyrichi* (Karsten); Etayo Serna, p. 54 [*partim*], pl. 1, figs 1-3; text-figs 4, 8–9; *non* text-figs 5, 7 [? = *K. beyrichi* (Karsten)].
1978 *Karsteniceras beyrichi* (Karsten); Wiedmann, pl. 4, fig. 2.

Holotype. GPIT 1719/2 (Pl. 1, figs 4–5); Upper Barremian; Barranco de las Higueras, Sierra Mediana, Subbetic, Spain.

Other material. Three paratypes (GPIT 1719/11–13); Barremian; Villa de Leiva, Colombia.

Diagnosis. Criocone with rounded whorl section, simple uniform ribs with marginal tubercles or thickening of ribs, and distinct siphonal furrow.

Description. The rounded whorl section of the criocone whorl is somewhat broader than high. The simple ribs are prorsiradiate at first (except the smooth first quarter whorl) changing finally to rectiradiate and rursiradiate. At first, ribs cross the venter uninterrupted; after one and a half whorls the first marginal tubercles or thickenings appear. At adult age, ribs are of unequal strength; the ventral furrow on the living chamber disappears. The last whorls have 42–50 ribs. The suture-line (Text-fig. 1c) is usually poorly incised and *L* is broadly rounded. *E* has a distinct median saddle which can, however, vary in width (Text-fig. 2). The other lobes are undivided. The saddles are symmetrically bipartite.

Measurements. The holotype measures 17 mm in maximum diameter (last suture at D = 10·5 mm). The largest specimen known (Etayo Serna 1968, pl. 1, fig. 1) has a final D of 40 mm.

Remarks. Karsteniceras ibericum sp. nov. is easily distinguished from its relatives by the distinct ventral furrow and the density of ribs.

Occurrence. Known from the Upper Barremian of Sierra Mediana, Subbetic, southern Spain, from the Lower to Upper Barremian transition at Ranzenberg, Drusberg Beds, Vorarlberg, Austria, and from deposits of a similar age at Villa de Leiva, Colombia.

Karsteniceras beyrichoide sp. nov.

Plate 1, figures 6–8, Text-figure 3A

1883 *Crioceras* (*Leptoceras*) *Beyrichi* Karst.; Uhlig, p. 272, pl. 32, figs 4–6, ?8.
1960 *Leptoceras beyrichi* Karsten; Drushtchic, p. 295, pl. 40, fig. 4.
1976 *Karsteniceras aff. beyrichi* (Karsten); Avram, p. 34, pl. 3, fig. 9.

Holotype. GBAW 3911 (Pl. 1, fig. 7); Upper(?) Barremian; Nýdek, Silesian Unit, Czech Republic. The original of *Crioceras* (*Leptoceras*) *beyrichi* (*sensu* Uhlig 1883, pl. 32, fig. 4).

Other material. GBAW 3902, 1883/4/118, BSM AS III 178, the three specimens figured by Uhlig (1883, pl. 32, figs 5–6, 8).

Diagnosis. Small-sized criocones with weak torsion of the shell. Whorl section subrectangular, probably as broad as high. The lateral sides are flat, as is the broad venter which carries a shallow siphonal furrow. Initial coil unknown; thereafter, sculpture consists of single sharp ribs as broad as the intervals. On the living chamber ribbing becomes less crowded. Marginal tubercles may be present or not; they are, moreover, of variable strength. Suture-line (Text-fig. 3A) is very simple with goniatitic lobes and bipartite saddles.

Measurements. The holotype has a final diameter of 39 mm, half whorl (?) of living chamber included, H_{max} = 10 mm. The last whorl is covered by 61 ribs. The most complete specimen, GBAW 3902 (Uhlig 1883, pl. 39, fig. 5), has a D_{max} = 30 mm; at D 26·3 mm, H is equivalent to 6·4 mm, U = 16 mm. The last whorl carries 64 ribs.

Remarks. Restudy of Uhlig's (1883, pl. 32, fig. 5) specimen GBAW 3902 has shown that it is formed by two living chambers placed in opposite directions, both of the same species. One of these specimens shows parts of the last suture-line. Another specimen (GBAW 1883/4/118; Uhlig 1883, pl. 32, fig. 8) cannot be included in *K. beyrichoide* with certainty; the ribs are less frequent than usual and carry pronounced marginal tubercles.

The present species can be distinguished from *K. beyrichi* by the differing ribbing on the living chamber and near the mouth border.

Occurrence. At present, *K. beyrichoide* sp. nov. is known with certainty only from the Upper(?) Barremian of Nýdek, Silesian Unit, Outer Carpathians, Czech Republic. Doubtfully included are specimens, possibly from the same stratigraphical level, from the Outer Dacidian Nappe, Roumania, and from the Kuma River, North Caucasus.

Karsteniceras pumilum (Uhlig, 1883)

Plate 1, figure 9; Plate 2, figures 3–4

1860 *Ancyloceras Escheri* Ooster, pl. 37, figs 3–4 only.
1883 *Crioceras* (*Leptoceras*) *pumilum* Uhlig, p. 270, pl. 29, figs 4–6.
1902 *Crioceras* (*Leptoceras*) *pumilum* Uhlig; Sarasin and Schöndelmayer, p. 147, pl. 20, fig. 4.
?1926 *Leptoceras cfr. pumilum* Uhlig; Yabe *et al.*, p. 73, pl. 15, fig. 20.
1938 *Leptoceras parvulum* Uhlig; Roman, pl. 35, figs 335–336.
1957 *Leptoceras pumilum* Uhlig; Wright, p. L211.
1958 *Leptoceras parvulum* Uhlig; Luppov and Drushtchic, pl. 48, figs 6–7.
1962 *Leptoceras pumilum* Uhlig; Manolov, p. 532.
?1962 *Leptoceras pumilum* Uhlig; Akopyan, p. 205, pl. 1, fig. 5.
1966 *Leptoceratoides pumilus* (Uhlig); Thieuloy, p. 289.

1969 *Leptoceras pumilus* Uhlig; Wiedmann, pl. 2, fig. 2.
1972 *Leptoceras pumilus* (Uhlig); Vašíček, p. 54, pl. 4, fig. 5.
1972 *Leptoceras pumilum* Uhlig; Wiedmann, pl. 1, fig. 2.
1976 *Leptoceratoides pumilus* (Uhlig); Avram, p. 33, pl. 4, fig. 1.
1984 *Leptoceras pumilum* Uhlig; Avram and Kusko, p. 14, pl. 2, fig. 8.
1987 *Leptoceratoides pumilus* (Uhlig); Matsukawa, p. 349.
1990 *Karsteniceras subtile* (Uhlig); Vašíček, pl. 1, fig. 6.

Lectotype (designated by Thieuloy 1966). BSM AS III 96; Lower Barremian; Straconka, Poland. The original of *Crioceras* (*Leptoceras*) *pumilum* Uhlig (1883, pl. 29, fig. 4; Pl. 1, fig. 9).

Other material. The two paralectotypes of Uhlig (1883), specimens figured by Ooster (1860), and new discoveries from the Outer Carpathians (OSM B13035, VŠB T 4/17, and unregistered specimens).

Revised diagnosis. Becoming criocone after an advolute inner whorl. For a short period (at D = 12–15 mm) whorls may touch each other. First whorl smooth, becoming ribbed at 8 mm D. First shallow constrictions appear at D = 10–12 mm. While simple ribs are radiate at first, they change later to rursiradiate. Exceptionally some ribs bifurcate on the lateral side of living chamber. Constrictions increase in strength. Suture-line unknown.

Measurements. The specimens attain diameters of 30–35 mm.

Remarks. Karsteniceras pumilum differs from all other species of the genus in its frequent and distinct constrictions. *K. subtile* (Uhlig) is similar but has less frequent and less pronounced constrictions; ribbing starts earlier (D = 4 mm); looping of ribs occurs only in some specimens; also the final size is smaller.

The Japanese specimen (Yabe *et al.* 1926) shows marginal tubercles in addition to the specific characters of this species; its inclusion remains, therefore, uncertain.

Occurrence. Tichá and Trojanovice, Outer Carpathians of the Czech Republic; Straconka and Górki Wielkie, Outer Carpathians of Poland; Getic and Outer Dacidian Nappes, Carpathians of Roumania; and Veveyse, External Prealps of Switzerland. Uncertain are the occurrences in America and Japan. The age is undefined Barremian; the Silesian specimens seem to belong only to the lower portion of the Barremian.

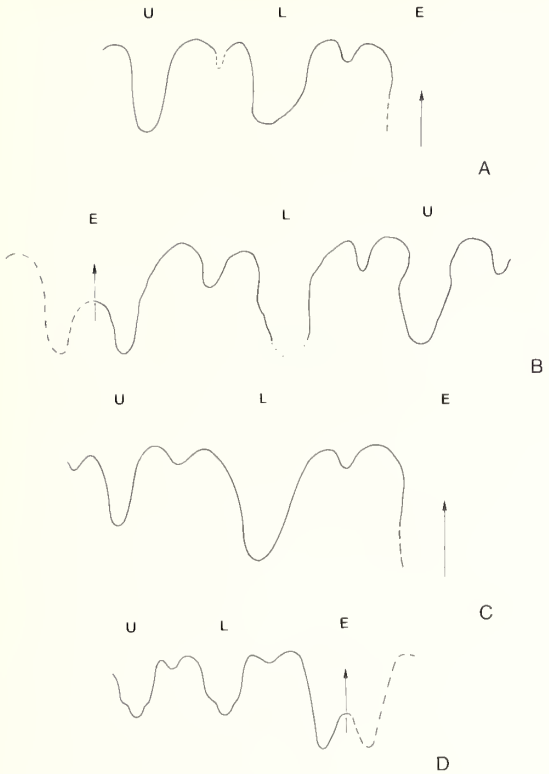
Karsteniceras subtile (Uhlig, 1883)

Plate 2, figures 5–8; Text-figure 3B

1883 *Crioceras* (*Leptoceras*) *subtile* Uhlig, p. 271, pl. 29, figs 7–9.
1966 *Leptoceratoides subtilis* (Uhlig); Thieuloy, p. 289.
?1967 *Leptoceras subtile* Uhlig; Dimitrova, p. 39, pl. 12, fig. 8; *non* fig. 7 [= *Karsteniceras balernaense* Rieber]; text-fig. 18.
1972 *Leptoceratoides subtilis* (Uhlig); Vašíček, p. 54, pl. 7, fig. 4.
1972 *Leptoceratoides* cf. *subtilis* (Uhlig); Vašíček, pl. 5, fig. 4; text-fig. 16.
1976 *Leptoceratoides subtilis* (Uhlig); Avram, p. 33.
?1977 ?*Karsteniceras* cf. subtilis (Uhlig); Myczyński, p. 155, pl. 4, fig. 5.
1984 *Leptoceras subtile* Uhlig; Avram and Kusko, p. 14, pl. 2, figs 6–7.
non 1990 *Karsteniceras subtile* (Uhlig); Vašíček, pl. 1, fig. 6 [= *Karsteniceras pumilum* (Uhlig)].
1991 *Karsteniceras subtile* (Uhlig); Manthey, pl. 2, fig. 1.

Lectotype (designated by Dimitrova 1967). GBAW 3949; Lower Barremian; Skalice, Czech Republic. The original of *Crioceras* (*Leptoceras*) *subtile* Uhlig (1883, pl. 29, fig. 9; Pl. 2, fig. 5 herein).

Other material. The two paralectotypes (GBAW 3948, 3901) of Uhlig (1883), and new discoveries from the Czech Carpathians (VŠB T 5/172), Eastern Alps (GPIT 1719/15) and the Subbetic of southern Spain (GPIT 1719/3).



TEXT-FIG. 3. Leptoceratoid suture-lines. A, *Karsteniceras beyrichoide* sp. nov., fragmentary suture-line at H = 6 mm; BSM AS III 178. B, *K. subtile* (Uhlig), external suture-line of lectotype at H = 2·2 mm; GBAW 3949. C, *K. hoheneggeri* sp. nov., fragmentary suture-line at H = 3 mm; BSM AS III 179. D, *K. hoheneggeri*, external suture-line at H = 6 mm; BSM AS III 454.

Revised diagnosis. Small criocones with rounded whorl section. Ribbing starts at D = 4 mm and consists of simple and looped ribs; at later stages ribs show ventrolateral thickening and seem to weaken on the venter. Near the mouth border ribbing becomes fine and dense. Weak constrictions, especially in early ages. Suture-line with trifid *L* and *U* and bipartite saddles (Text-fig. 3B).

Measurements. The lectotype has a maximum D of 19 mm. At D = 15, H_{max} = 4 mm (0·27), U = 8·5 (0·57). 24 R/2; in some specimens even more ribs occur.

Remarks. Special characters of *K. subtile* are its very small size, the occasional looping of ribs, and the dense and fine ribbing near the mouth border.

Occurrence. *Karsteniceras subtile* is presumably restricted to the Lower Barremian. Regionally, it is known from Tichá, Skalice and Nýdek, Outer Carpathians, Czech Republic; probably from Lietavská Lúčka, Central Carpathians of Slovakia; from the Getic and Outer Dacidian Nappes, Carpathians of Roumania; from Bad Ischl in the Austroalpine of Salzkammergut, Austria; and from Sierra del Valle, Subbetic of Spain. Published records from Bulgaria and Cuba are uncertain.

Karsteniceras hoheneggeri sp. nov.

Plate 2, figure 9; Plate 3, figures 1–3; Text-figure 3C–D

1883 *Crioceras* (*Leptoceras*) n. sp. ind. aff. *cristatum* d'Orbigny; Uhlig, p. 272, pl. 32, fig. 3.
1883 *Crioceras* (*Leptoceras*) n. sp. ind.; Uhlig, p. 272, pl. 32, fig. 7.
?1966 *Leptoceras beyrichi* (Karsten); Breskovski, p. 79, pl. 6, fig. 1.
?1967 *Karsteniceras beyrichi* (Karsten); Dimitrova, p. 9, pl. 12, fig. 6.

Holotype. BSM AS III 179; Upper(?) Barremian; Malenovice, Czech Republic. *Crioceras* (*Leptoceras*) n. sp. ind. aff. *cristatum* (d'Orbigny) of Uhlig (1883, pl. 32, fig. 3; Pl. 2, fig. 9).

Other material. BSM AS III 454, Hohenegger Collection, figured by Uhlig (1883). GPIT 1719/4, fragmentary specimen from Breggia, Southern Alps.

Diagnosis. Regular criocone coiling. Whorl section rounded with inflated lateral sides and flat to concave venter. In the adult, simple and strong ribs of unequal strength, with marginal thickening and concave venter. Three constrictions on the last half whorl. Suture-line with simple elements and broad *L*.

Measurements. The holotype has D_{max} = 38 mm; at D = 28·5 mm, H = 9 mm and U = 13·6 mm. On the last whorl, thirty eight ribs can be counted.

Remarks. *Karsteniceras hoheneggeri* sp. nov. is similar to *K. beyrichioide* sp. nov. and to *K. pumilum*. Its ribbing is, however, more pronounced and less crowded. *K. trinidadense* sp. nov. has a much finer ribbing with larger interspaces.

Occurrence. Known from the Upper(?) Barremian of Malenovice and Nýdek, Silesian Unit, Outer Carpathians, Czech Republic; and from the Upper Barremian of Breggia, Southern Alps, Switzerland. Uncertain is the inclusion of specimens from the Upper Barremian of Bulgaria.

Karsteniceras trinidadense sp. nov.

1954 *Leptoceras* sp. indet.; Imlay, p. 664, pl. 74, figs 16–17; *non* fig. 18.

Holotype. USMM 108726; Barremian; Tompire Bay, Trinidad; figured as *Leptoceras* sp. indet. by Imlay (1954, pl. 74, fig. 16).

Diagnosis. Small criocones with fine and dense ribbing and with marginal thickening. Ribs widely spaced, intervals four times as wide as ribs. Suture-line unknown.

Measurements. The holotype has a maximum diameter of 27 mm.

Remarks. The type material is rather poorly preserved in a phyllitic matrix, and is deformed. Whorl section and suture-line are unknown. The ribbing, which consists of fine and strong ribs with large interspaces, is however so different from all other *Karsteniceras* species that a specific separation can be proposed. The marginal thickening of ribs is not as obvious as mentioned by Imlay (1954). This is a typical *Karsteniceras*, even if the suture-line is unknown.

Occurrence. Lower part of Upper Barremian of Tompire Bay, Trinidad.

EXPLANATION OF PLATE 3

Figs 1–3. *Karsteniceras hoheneggeri* sp. nov. 1–2, BSM AS III 454; Upper? Barremian; Nýdek – Ostrá hora, Outer Carpathians, Czech Republic. 1, lateral and ventral views; ×1. 3, GPIT 1719/4; Upper Barremian; Breggia, Ticino, Switzerland; ×3.

Fig. 4. *Karsteniceras balernaense* Rieber, GPIT 1719/5; Upper Barremian; Breggia, Ticino, Switzerland; ×1.

Figs 5–12. *Hamulinites parvulus* (Uhlig). 5, BSM AS III 453, lectotype; Lower Barremian; Veřovice, Outer Carpathians, Czech Republic; ×1. 6, GPIT 1719/6; Lower Barremian; Bad Ischl, Salzkammergut, Austria; ×3. 7, VŠB Pi 1/12; Lower Barremian; Pindula near Frenštát p. R., Outer Carpathians, Czech Republic; ×2. 8, OSM B 13664; Lower Barremian; Angles, Haute Provence, France; ×2. 9, MHNP, d'Orbigny coll. 5428-1; Barremian; Escragnolles, Var, France; ×1·5. 10, SNM Z 21 125; Lower Barremian; Lietavská Lúčka, Central Western Carpathians, Slovakia; ×1. 11, GPIT 1719/7; Lower Barremian; La Querola near Cocentaina, Prebetic of Alicante, Spain; ×2. 12, GPIT 1719/8, same horizon and locality as fig. 11; ×3.

VAŠÍČEK and WIEDMANN, *Karsteniceras*, *Hamulinites*

Karsteniceras balernaense Rieber, 1977

Plate 3, figure 4

1967 *Leptoceras subtile* Uhlig; Dimitrova, p. 39 [*partim*], pl. 12, fig. 7; *non* fig. 8 [? = *K. subtile* Uhlig].
1977 *Karsteniceras balernaense* Rieber, p. 779, pl. 1, figs 1–7, text-fig. 2.
?1984 *Leptoceras*? cf. *barnaense* (Rieber); Avram and Kusko, p. 14, pl. 2, fig. 9.

Holotype. PIMUZ L/1584; Barremian; Balerna, Switzerland; figured by Rieber (1977, pl. 7, fig. 1).

Other material. GPIT 1719/5; a poorly preserved specimen from the southern Alps of Breggia Gorge, Switzerland.

Revised diagnosis. Small criocones, probably with weak torsion. Single sharp uniform ribs from a D of 3·5 mm. 52 ribs per whorl. No tubercles. Venter unknown. Suture-line simple.

Remarks. The uniform type of ribbing up to the mouth border separates *K. balernaense* from *K. subtile*; the lack of constrictions distinguishes this species from *K. pumilum*. *K. polieri* Myczyński (1977) differs in having bifurcating ribs.

Occurrence. Originally described from the Upper Barremian of Breggia Gorge near Balerna, Ticino, Switzerland; known also from the Lower Barremian of Kraptshene, Prebalkan, Bulgaria, and probably the Romanian Southern Carpathians.

Karsteniceras polieri Myczyński, 1977

1977 *Karsteniceras polieri* Myczyński, p. 154, pl. 4, figs 1, 3, 7.

Holotype. IGPH No. 2556b; Lower Barremian; Polier, Cuba; figured by Myczyński (1977, pl. 4, fig. 7).

Revised diagnosis. Small criocones with dense and fine ribbing. The prorsiradiate ribs bifurcate periodically at the umbilical border. No constrictions.

Remarks. This species resembles both *K. subtile* and *K. balernaense* but it differs in having bifurcating ribs.

Occurrence. Lower Barremian of the Polier Formation, Sierra del Rosario, Cuba.

Karsteniceras asiaticum (Yabe and Shimizu, 1926)

1926 *Leptoceras asiaticum* Yabe and Shimizu in Yabe *et al.*, p. 73, pl. 15, fig. 21.
1966 *Leptoceratoides asiaticus* (Yabe and Shimizu); Thieuloy, p. 289.
1988 *Karsteniceras asiaticum* (Yabe and Shimizu); Matsukawa, p. 399, fig. 3: 4–6; fig. 4.

Holotype. IGPS 22849; Lower Barremian; Ishido, Japan; figured by Yabe and Shimizu (*in* Yabe *et al.* 1926, pl. 15, fig. 21).

Revised diagnosis. Small criocones with subrectangular whorl section. Ribs are fine and dense at the beginning, later they show broad interspaces and become rursiradiate on the living chamber. At later stages, about twenty ribs per half whorl. Ventral side with weak depression.

Remarks. While ribs cross the ventral depression in *K. asiaticum*, they are interrupted on the venter of the similar *K. obatai* Matsukawa.

Occurrence. Lower Barremian of Ishido, Hondo, Japan.

Karsteniceras obatai Matsukawa, 1987

1926 *Ancyloceras*? sp. indet.; Yabe *et al.*, p. 71, pl. 15, figs 12–13.
1987 *Karsteniceras obatai* Matsukawa, p. 349, figs 1–2; 3, 1–4; 4.
1988 *Karsteniceras obatai* Matsukawa; Matsukawa, p. 401, fig. 3: 7–9; fig. 5.

Holotype. NSMT–PM 9589; Lower Barremian; Isejigauara, Japan; figured by Matsukawa (1987, fig. 3: 3).

Diagnosis. Small criocones with smooth initial whorl. From a diameter of 10 mm simple and rectiradiate ribs with marginal tubercles. Ribs are interrupted at a narrow siphuncular furrow. Suture elements simplified.

Remarks. In *Karsteniceras obatai* marginal tubercles and the siphuncular furrow disappear on the living chamber. The differences between *K. obatei* and *K. asiaticum* are given above.

Occurrence. Lower Barremian of Isejigauara, Hondo, Japan.

Karsteniceras? *filicostatum* (Stahlecker, 1935)

1935 '*Toxoceras*' *filicostatum* Stahlecker, p. 286, pl. 14, fig. 16.
1966 *Leptoceratoides filicostatus* (Stahlecker); Thieuloy, p. 289.

Holotype. GPIT 493/14/16; Lower(?) Barremian; Maio, Cape Verde Islands; figured by Stahlecker (1935, pl. 14, fig. 16).

Revised diagnosis. Middle-sized criocones with open coil. Sculpture consists of fine, dense and radiate ribs. Each third/fourth rib with weak marginal tubercles. Suture-line unknown.

Remarks. *Karsteniceras*? *filicostatum* resembles the likewise dubious *K.*? *heeri* (Ooster) in coiling. However, the latter has coarser ribbing. Like *K.*? *heeri*, the present species is too poorly known (the suture-line is unknown) to be included in *Karsteniceras* with certainty.

Occurrence. Lower(?) Barremian of Maio, Cape Verde Islands.

Karsteniceras? *heeri* (Ooster, 1860)

1860 *Ancyloceras Heeri* Ooster, p. 32 [*partim*], pl. 38, figs 5, ? 1–3; *non* fig. 4 [= *Anahamulina distans* Vašíček].
1902 *Crioceras* (*Leptoceras*) *Heeri* Ooster; Sarasin and Schöndelmayer, p. 149 [*partim*], pl. 20, fig. 2; *non* fig. 3 [= *A. distans* Vašíček].

Lectotype (designated herein). NMB 5683; Barremian; Veveyse, Switzerland; figured by Ooster (1860, pl. 38, fig. 5).

Revised diagnosis. Middle-sized criocones(?), whorl slowly increasing in height. Ribs as broad as interspaces, radiate on lateral sides, becoming prorsiradiate and weakly inflated at the umbilical margin. Last whorl with weak constrictions. Suture-line unknown.

Measurements. D_{max} = 40 mm, H = 8·0 mm (0·20), U = 27·5 mm (0·69). R/2 > 50.

Remarks. Due to the fragmentary preservation of the paralectotypes, it is unknown whether *K.*? *heeri* is criocone throughout or has the elliptical coiling of *Veveysiceras*. In this case, Ooster's (1860, pl. 38, figs 1–3) juveniles would have to be included.

According to Sarasin and Schöndelmayer (1902, p. 149), some specimens of *Ancyloceras sabaudianum* Pictet and Loriol (1858, pl. 6, figs 6, 9) should be referred to *K.*? *heeri*; their juvenile coils are, however, criocone.

K.? filicostatus (Stahlecker) has a coiling similar to the present species, but has a finer and denser ribbing.

Occurrence. Barremian of Veveyse, External Prealps, Switzerland.

Genus HAMULINITES Paquier, 1901

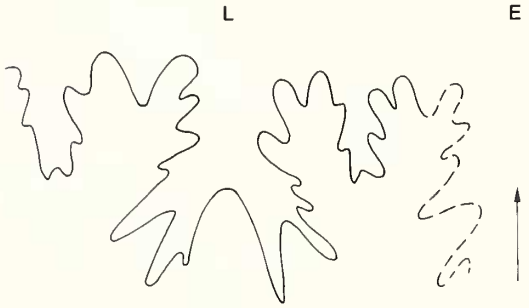
[= *Leptoceras* Uhlig, 1883 [*partim*]; *Eoleptoceras* Manolov, 1962; *E.* (*Tzankoviceras*) Manolov, 1962; *E.* (*Wrightites*) Manolov, 1962.]

Type species. Hamulina munieri Nicklès, 1894 [= *Leptoceras parvulum* Uhlig, 1883.].

Revised diagnosis. Small-sized ancylocones; first two whorls advolute, then slowly uncoiling (proversum according to Vašíček 1972, fig. 12) towards the final hook which is mainly formed by the living chamber. Simple ribs without tuberculation. Suture-line with four elements (*E, L, U, I*), with relatively simple outlines.

Remarks. Hamulinites comprises small-sized ancyloceratids, but there are no early criocone whorls and no marginal spines; suture elements remain simple, but are more complicated than in *Karsteniceras.* Due to its ancylocone coiling, *Hamulinites* is easy to separate from the other representants of the Leptoceratoidinae. There is, however, a certain similarity to small-sized hamulinids, above all to *Hamulina varusensis* d'Orbigny, 1850 (see d'Orbigny 1852, p. 221, pl. 5, figs 4–6; Cottreau 1937, p. 72, pl. 80, figs 3–6). After studying the four syntypes of *H. varusensis* preserved in the MHNP, we can assume that d'Orbigny's complete specimen (1852, pl. 5, fig. 4) is a reconstruction based on the fragments known. These bear a complicated suture-line (see Cottreau 1937, p. 72) of hamulinid configuration. *H. varusensis* is, therefore, referred to *Anahamulina* Hyatt. The most complete syntype (Cottreau, 1937, pl. 80, fig. 4), however, is different from d'Orbigny's figures and is here included in *Hamulinites parvulus* Uhlig.

Anahamulina distans Vašíček (1972, pl. 15, fig. 4) also shows similarity with *Hamulinites* in size and coiling, but has a very different, more complicated suture-line (see Text-fig. 4). This complicated



TEXT-FIG. 4. Fragmentary suture-line of *Anahamulina distans* Vašíček, at H = 6·5 mm; BSM AS III 452.

suture-line, generally larger size and, in most species, constrictions on the hook, are the main differences distinguishing *Anahamulina* from *Hamulinites.*

The middle-sized *Ancyloceras sabaudianum* Pictet and Loriol (1858) also exhibits similarities with the genus *Hamulinites*, as does '*Hamulinites*' *norteyi* Myczyński and Triff, 1986. However, the former shows a criocone initial coil and marginal spines unknown from *Hamulinites*, while the latter exhibits a slightly heteroceratid coiling and is therefore included in *Eoheteroceras* gen. nov.

Another doubtful group of forms was described by Drushtchic (1960, pl. 39, fig. 3) as '*Leptoceras biplex*' von Koenen. These are small-sized ancylocones with true ancyloceratid sculpture, i.e. three rows of tubercles on the ribs of both arms. The position of these forms cannot be clarified without

studying Russian specimens. As a consequence, only the following species remain attributable to *Hamulinites: H. parvulus* (Uhlig), *H. fragilis* (Uhlig) and *H. assimilis* (Uhlig).

Distribution. Mainly Lower Barremian, rare in the Upper Barremian; Outer Western Carpathians of the Czech Republic and Poland; Central Carpathians of Slovakia; Carpathians of Roumania; Bulgaria; Austroalpine of Austria; Prealps of Switzerland; Vocontian Trough, France; Subbetic of Spain; Cuba (?).

Hamulinites parvulus (Uhlig, 1883)

Pl. 3, figures 5–12; Text-figure 5A

?1860 *Ancyloceras Fourneti* Astier; Ooster, p. 22, pl. 34, fig. 10; *non* figs 9, 11.
1883 *Crioceras* (*Leptoceras*) *parvulum* Uhlig, p. 273, pl. 29, figs 3, 10.
1894 *Hamulina Munieri* Nicklès, p. 59, pl. 5, figs 7–8, text-fig. 42.
1902 *Hamulina parvula* Sarasin and Schöndelmayer, p. 166, pl. 23, figs 4–5.
1937 *Hamulina Varusensis* d'Orbigny; Cottreau, p. 72, pl. 80, fig. 3; *non* figs 4–6.
non 1938 *Leptoceras parvulum* Uhlig; Roman, pl. 35, figs 335–336 [= *Karsteniceras pumilum* (Uhlig)].
1957 *Hamulinites munieri* (Nicklès); Wright, p. L215.
non 1958 *Leptoceras parvulum* Uhlig; Luppov and Drushtchic, pl. 48, figs 6–7 [= *Karsteniceras pumilum* (Uhlig)].
1962 *Eoleptoceras* (*Wrightites*) *parvulum* (Uhlig); Manolov, pp. 532, 534, pl. 75, figs 3, 11–12.
1962 ?*Eoleptoceras* (*Tzankoviceras*) *assimilis* (Uhlig); Manolov, pl. 74, figs 3–4.
1962 *Eoleptoceras* (*Tzankoviceras*) *tzankovi* Manolov, p. 533, pl. 75, figs 2, 7–8.
1962 *Eoleptoceras* (*Wrightites*) *parvulum kraptshenensis* Manolov, p. 535, pl. 75, figs 4–6, text-fig. 1C.
1962 *Eoleptoceras* (*Wrightites*) *wrighti* Manolov, p. 535, pl. 75, figs 9–10, text-fig. 1B.
1963 *Hamulinites munieri* (Nicklès); Wiedmann, p. 108, pl. 1, fig. 3, text-fig. 2.
1966 *Eoleptoceras parvulum* (Uhlig); Thieuloy, p. 289.
1966 *Anahamulina varusensis* (d'Orbigny); Breskovski, p. 82, pl. 4, fig. 2.
1967 *Eoleptoceras* (*E.*) *parvulum* (Uhlig); Dimitrova, p. 36, pl. 17, fig. 7, text-fig. 16.
1967 *Eoleptoceras* (*E.*) *varusensis* (d'Orbigny); Dimitrova, p. 36, pl. 17, fig. 8.
1967 *Eoleptoceras* (*s.lato*) *wrighti* Manolov; Dimitrova, p. 36, pl. 16, fig. 8.
1967 *Eoleptoceras* (*Tzankoviceras*) *tzankovi* Manolov; Dimitrova, p. 37, pl. 18, figs 7–9.
1967 *Eoleptoceras* (*Tzankoviceras*) *assimilis* (Uhlig); Dimitrova, p. 37, pl. 18, fig. 10.
non 1967 *Eoleptoceras* (*Wrightites*) *parvulum* (Uhlig); Nagy, p. 68, pl. 3, fig. 3 [= Crioceratitinae juv.]
1972 *Hamulinites parvulus* (Uhlig); Vašíček, p. 53, pl. 7, fig. 2, text-fig. 15.
1976 *Hamulinites cf. parvulus* (Uhlig); Avram, p. 34, pl. 4, fig. 2.
?1986 *Hamulinites aff. parvulus* (Uhlig); Myczyński and Triff, p. 126, pl. 2, figs 1, 9, 15.
1990 *Hamulinites parvulus* (Uhlig); Vašíček, pl. 1, fig. 4.

Lectotype (designated by Manolov 1962). BSM AS III 453; Lower Barremian; Veřovice (Wernsdorf), Czech Republic; figured by Uhlig (1883, pl. 29, fig. 3).

Other material. OSM B 13 033, VŠB Pi 1/12, K 8/014, OT 5/18 and unregistered fragments, about twenty specimens from the Czech Outer Carpathians; SNM Z-21 125 and unregistered fragments, Central Carpathians of Slovakia; OSM B 13 664, Angles and MHNP – d'Orbigny coll. 5428-1, Escragnolles, southern France; GPIT 1719/7, 1719/8, Prebetic of Alicante; GPIT 1719/6, Bad Ischl, Austroalpine and the material from Sarasin and Schöndelmayer (1902) described as '*Hamulina parvula*'.

Revised diagnosis. Small ancylocones, eventually with heteroceratid torsion of the initial coil. Shell initially smooth, then with single sharp untubercled ribs crossing venter without interruption. Suture-line with relatively high and smooth median saddle in *E*; *L* and *U* trifid, saddles simple and bipartite (Text-fig. 5A).

Remarks. Hamulinites parvulus is a variable species, exhibiting variations in size (D around 30 mm), coiling of the initial coil, separation of the two final arms, and strength and density of ribbing. Therefore, a number of Manolov's (1962) species have to be synonymized with *H. parvulus*; extreme

forms, which have criocone initial coils, were described as '*Eoleptoceras assimile*' (Uhlig) by Manolov (1962, pl. 74, figs 3–4). Unfortunately, none of the specimens with unknown suture-lines can be determined generically.

Hamulina parvula, described by Sarasin and Schöndelmayer (1902) from the Barremian of Châtel St Denis, is very similar in coiling, size and sculpture, but was separated due to the existence of two rows of tubercles on the living chamber. After revision of the two specimens figured, it is obvious that there is not even a single row of tubercles. One of the specimens (pl. 23, fig. 4) was, however, an injured and restored living chamber margin. Moreover, fragments of the suture-line visible exhibit simplified lobes and saddles. In consequence, these specimens are included in *H. parvulus*.

H. fragile can easily be separated by its typical reduction of ribbing near the mouth border, while *H. assimilis* has stronger ribs on the larger and more robust shell.

Occurrence. A cosmopolitan and mainly Lower Barremian species which was first described from Veřovice and Lipnik, Outer Western Carpathians of the Czech Republic and Poland. Also recorded from: Escragnolles, southern France; Querola, Prebetic of southern Spain; Châtel St Denis/Switzerland; Kraptshene, Prebalkan, Bulgaria; Ceahlau Nappe East Carpathians of Roumania; and Cuba(?). Additionally, we have collected the species in the lower part of the Barremian type section at Angles, southern France; the Lower Barremian of Querola, Prebetic of Spain; the Austroalpine beds near Bad Ischl, Austria,; and in the Outer Carpathians (Tichá, Trojanovice, Pindula), Czech Republic and Central Western Carpathians (Lietavská Lúčka, Butkov, Zrázy), Slovakia.

Hamulinites fragilis (Uhlig, 1883)

Plate 4; figures 1–2; Text-figure 5B

1860 *Ancyloceras Escheri* Ooster, p. 29 [*partim*], pl. 37, fig. 2; *non* figs 1, 7–9, ?6 [= *Veveysiceras escheri* (Ooster)]; *non* figs 3–4 [= *Karsteniceras pumilum* (Uhlig)]; *non* fig. 5 [= *Crioceratites*? sp.].

1883 *Crioceras* (*Leptoceras*) *fragile* Uhlig, p. 274, pl. 29, fig. 11.

1902 *Crioceras* (*Leptoceras*) *Escheri* Ooster; Sarasin and Schöndelmayer, p. 148 [*partim*], pl. 19, fig. 4; *non* fig. 5 [= *Crioceratites*? sp.]; *non* fig. 6 [= *Veveysiceras escheri* (Ooster)].

1984 *Eoleptoceras* (*E.*) *aff. fragile* (Uhlig); Avram and Kusko, p. 14, pl. 2, fig. 5.

Neotype (designated herein). OSM-B 13663; Lower Barremian; Nýdek, Silesian Unit, Czech Republic (Pl. 4, fig. 1). Uhlig's type specimen from the same area (Lipnik) can be located neither at GBAW nor at BSM, and is thus considered lost.

Other material. The NMB specimens which Ooster (1860) described as *Ancyloceras escheri*.

EXPLANATION OF PLATE 4

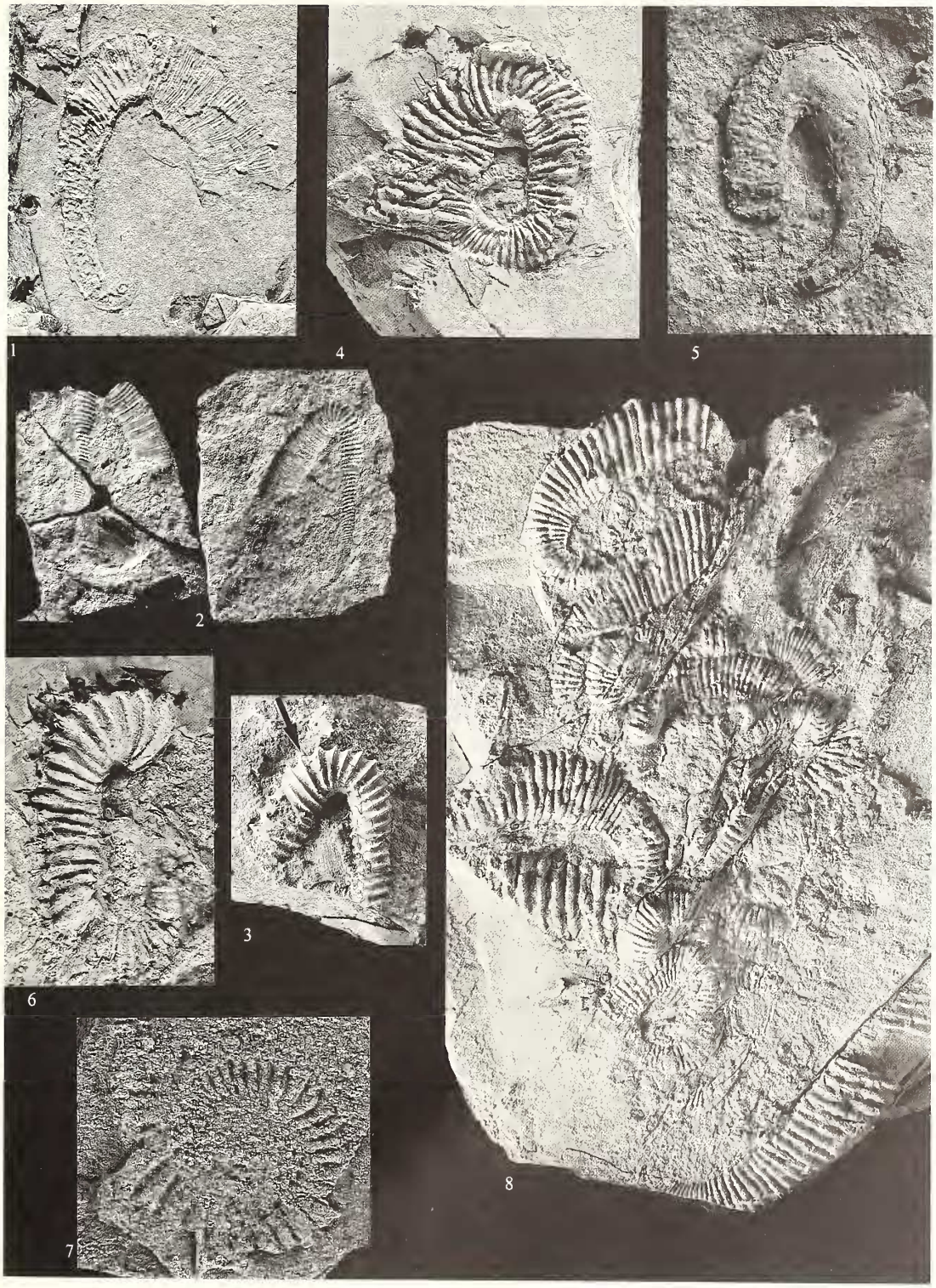
Figs 1–2. *Hamulinites fragilis* (Uhlig). 1, OSM B 13663, neotype; Lower Barremian; Nýdek, Outer Carpathians, Czech Republic; ×2. 2, NMB 5725*a*; Lower Barremian; Veveyse, Vaud, Switzerland; part (left) and counterpart (right); ×1.

Fig. 3. *Hamulinites assimilis* (Uhlig). BSM AS III 177, holotype; Upper Barremian; Mistřovice, Outer Carpathians, Czech Republic; ×1.

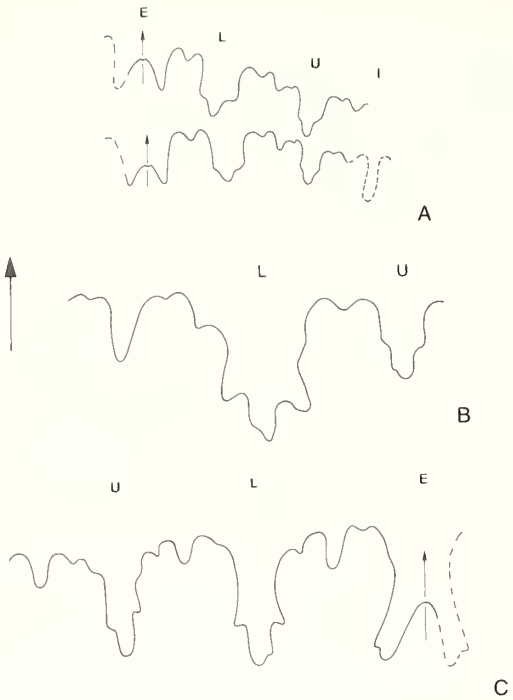
Figs 4–5. *Eoheteroceras silesiacum* gen. et sp. nov. 4, GBAW 3938, holotype; Lower Barremian; Górki Wielkie, Outer Carpathians, Poland; ×1·5. 5, GPIT 1719/9; Lower Barremian, La Querola near Cocentaina, Prebetic of Alicante, Spain; ×2.

Figs 6–7. *Eoheteroceras uhligi* (Vašíček). 6, VŠB OT 5/30; Lower Barremian; Ostravice, Outer Carpathians, Czech Republic; ×2. 7, GPIT 1719/10; Upper Barremian; Breggia, Ticino, Switzerland; ×2·5.

Fig. 8. *Manoloviceras saharievae* (Manolov). OSM B 13039; Lower Barremian; Shaft Frenštát 5, at 294 m depth, Outer Carpathians, Czech Republic; 'nest' of mostly juvenile individuals; ×2.



VAŠÍČEK and WIEDMANN, *Hamulinites*, *Eoheteroceras*, *Manoloviceras*



TEXT-FIG. 5. Leptoceratoid suture-lines. A, suture-lines of *Hamulinites parvulus* (Uhlig) at H = 3·3 and 3·5 mm; BSM AS III 453. B, fragmentary suture-line of *H. fragilis* (Uhlig) at H = 3·5 mm; NMB 5725a. C, external suture-line of *H. assimilis* (Uhlig) at H = 6·2 mm; BSM AS III 177.

Revised diagnosis. Small ancylocones. Initial coil gently curved; with final hook. Shell initially smooth, then with sharp and fine simple ribs, becoming replaced by fine and dense growth-lines on the central hook (= living chamber?). Suture-line of *Hamulinites* type.

Measurements. The neotype has D_{max} = 22 mm, the retroversum measures 15 mm, H_{max} = 7 mm. The diameter of the coiled first whorl is 2 mm.

Remarks. *Hamulinites fragilis* is easily separated, even when juvenile or fragmentary, from the similar *Veveysiceras escheri* (Ooster) by its fine ribbing.

Occurrence. Lower Barremian. Lipnik and Nýdek, Outer Western Carpathians, Poland and Czech Republic; Veveyse, External Prealpes, Switzerland; and probably from Romania.

Hamulinites assimilis (Uhlig, 1883)

Plate 4, figure 3, Text-figure 5C

1883 *Crioceras* (*Leptoceras*) *assimile* Uhlig, p. 272, pl. 32, fig. 9.
1962 *Eoleptoceras* (*Tzankoviceras*) *assimilis* (Uhlig); Manolov, p. 533 [*partim*], pl. 73, figs 7–8; *non* pl. 74, figs 3–4 [? = *Hamulinites parvulus* (Uhlig)].
non 1967 *Eoleptoceras* (*Tzankoviceras*) *assimilis* (Uhlig); Dimitrova, p. 37, pl. 18, fig. 10 [? = *Hamulinites parvulus* (Uhlig)].
non 1967 *Eoleptoceras* (*Tzankoviceras*) *assimilis* (Uhlig); Nagy, p. 67, pl. 3, fig. 4 [? = Crioceratitinae juv.].

Holotype. BSM AS III 177; Upper(?) Barremian; Mistřovice, Silesian Unit, Czech Republic; figured by Uhlig (1883, pl. 32, fig. 9).

Revised diagnosis. Middle-sized hamulinicone, with simple sharp ribs crossing venter uninterrupted. Interspaces twice as wide as ribs. On the phragmocone ribs project; on the possibly short living

chamber (= retroversum) ribs are radiate. Suture-line relatively complicated; lobes and saddles with fine incisions.

Measurements. The fragmentary proversum measures 24 mm, H_{max} = 6 mm. Length of retroversum is 19 mm, with H_{max} = 8 mm.

Remarks. A relatively large-sized leptoceratoid. Size and more complicated suture-line facilitate distinction from other *Hamulinites* species. The species is similar to *Anahamulina distans* Vašíček and '*Hamulina*' *varusensis* d'Orbigny, both of which have much more complicated suture-lines.

Specimens described from Bulgaria differ in ribbing, and approach *H. parvulus* (Uhlig). Revision of the Hungarian material (Nagy 1967) leads to the conclusion that these forms are fine-ribbed juveniles of ?Crioceratitinae; traces of suture-lines show strong denticulation.

Occurrence. Upper(?) Barremian, Mistřovice, Outer Western Carpathians, Czech Republic.

Genus VELEZICERAS Wright, 1957

[= *Orbignyceras* Royo y Gómez, 1945 p. 462 (non Gérard and Contaut, 1936)].

Type species. Orbignyceras veleziensis Royo y Gómez, 1945. Barremian, Vélez-Chipatá, Colombia.

Revised diagnosis. Straight to gently curved shells with elliptical whorl section. Simple and projected sharp ribs without any tubercle; eventually with faint periodic constrictions. Suture-line simple.

Remarks. Despite the fact that neither the early nor the late growth stages are known, a series of forms with bochianitid coiling are included in Leptoceratoidinae. Inclusion is based on the simplified suture-line: *E* is divided by a small median saddle, lobes are undivided, saddles are bifid. This represents the most primitive (reduced?) leptoceratoid suture-line.

Veleziceras was previously (Wiedmann 1973) included in *Karsteniceras*, but may better be considered distinct. It approaches in coiling *Hamulinites*, but has a much more complicated suture-line. Besides the type species, *V. hennigi* (Stahlecker) is also included in *Veleziceras*.

Distribution. Barremian of Colombia and Maio, Cape Verde Islands.

Veleziceras veleziense (Royo y Gómez, 1945)

1945 *Orbignyceras veleziensis* Royo y Gómez, p. 462, pl. 71, fig. 1*d–e*; text-fig. 2.
1957 *Veleziceras veleziense* (Royo y Gómez); Wright, p. L210.

Lectotype (designated herein). SGNB specimen figured as *Orbignyceras veleziense* by Royo y Gómez (1945, pl. 71, fig. 1*e*); Barremian, Vélez-Chipatá, Colombia.

Diagnosis. As for the genus.

Remarks. Of the two specimens Royo y Gómez (1945) described as the 'holotype', the larger one is here chosen as the lectotype.

Occurrence. Barremian of Vélez-Chipatá, Colombia.

Veleziceras hennigi (Stahlecker, 1935)

1935 *Bochianites hennigi* Stahlecker, p. 287, pl. 14, figs 18–20.

Lectotype (designated herein). GPIT 493/14/18; Barremian; Maio, Cape Verde Islands; figured by Stahlecker (1935, pl. 14, fig. 18).

Revised diagnosis. Middle-sized, nearly straight shells with simple, slightly prorsiconcave ribs. Width of ribs equal to interspaces. Suture-line unknown.

Remarks. This poorly known species is included in *Veleziceras* with some doubt. *V. hennigi* is similar to the type-species, but can be separated by its more concave ribbing and the absence of constrictions.

Occurrence. Barremian (presumably Lower) of Maio, Cape Verde Islands.

Genus EOHETEROCERAS gen. nov.

Type species. Eoheteroceras silesiacum sp. nov.

Diagnosis. Small-sized ancylocones with strong simple ribs. Juvenile coil criocone-trochospiral. Retroversum overlapping juvenile coil.

Description. First whorl unknown, juvenile whorl forming an indistinct trochospiral coil which can be covered by the final retroversum. This makes clear differentiation and interpretation of the juvenile coil difficult. Adult age ancylocone, with usually long retroversum. It can be assumed that the ancylocone stage underwent torsion to avoid collision of the mouth border with the juvenile part. Due to sedimentary compaction in the complete specimens, it is hard to estimate the distance between both parts. The shell is covered by simple, strong and prorsiradiate ribs. Suture-line unknown.

Remarks. The juvenile stage separates *Eoheteroceras* gen. nov. from *Hamulinites*. *Heteroceras* d'Orbigny can easily be separated by the distinctly helicoidal initial part and, in most cases, by its larger size. Besides the type species, *Eoheteroceras* includes *E. norteyi* (Myczyński and Triff), *E. uhligi* (Vašíček), and *E.*? *multicostatum* (Stahlecker).

Distribution. Barremian of the Outer Carpathians of Poland and the Czech Republic; Southern Alps of Switzerland; Prebetic of Spain; Cuba; and probably Maio, Cape Verde Islands.

Eoheteroceras silesiacum sp. nov.

Plate 4, figures 4–5

1883 *Leptoceras* n. f. ind.; Uhlig, p. 274, pl. 29, fig. 2.

Holotype. GBAW 3938; Lower(?) Barremian; Górki Wielkie (Gurek), Poland (Pl. 4, fig. 4); figured by Uhlig (1883, pl. 29, fig. 2).

Other material. GPIT 1719/9; Lower Barremian; La Querola, Spain.

Diagnosis. Small-sized elliptical shell with open criocone-trochospiral juvenile coil and ancylocone adult hook. Retroversum long. Ribbing sharp and simple.

Description. Elliptically coiled small form with long retroversum and ribs as wide as interspaces.

Measurements. D_{max} of the holotype = 23·5 mm, the deformed H_{max} 10·5 mm.

Remarks. *Eoheteroceras norteyi* is very similar to the present species, but its coiling is less elliptical and the ribbing is finer. *E. uhligi* can be distinguished by its more involute juvenile coil and a much shorter retroversum. *E.*? *multicostatum* is larger than the other species but its inclusion in the present genus remains doubtful due to its very poor preservation.

Occurrence. Presumed Lower Barremian from Górki Wielkie, Polish Outer Western Carpathians, and Querola, Prebetic, Spain.

Eoheteroceras norteyi (Myczyński and Triff, 1986)

1986 *Hamulinites norteyi* Myczyński and Triff, 1986, p. 127, pl. 1, fig. 8; pl. 3, fig. 6.

Holotype. MPMS-R AM-88/2; Barremian; Nortey, Pinar del Rio Province, Cuba; figured by Myczyński and Triff (1986, pl. 1, fig. 8).

Revised diagnosis. Small-sized ancylocone with criocone juvenile coil and long retroversum. Interspaces much wider than sharp simple ribs.

Remarks. Despite the unknown suture-line, *E. norteyi* shows all of the characteristics of *Eoheteroceras*. The mode of coiling contrasts with that of *Hamulinites* insofar as the retroversum overlaps the criocone juvenile coil.

Occurrence. Barremian of Cuba.

Eoheteroceras uhligi (Vašíček, 1981)

Plate 4, figures 6–7

1883 *Heteroceras* n. f. ind.; Uhlig, p. 274, pl. 32, fig. 10.
1981 *Heteroceras uhligi* Vašíček, p. 123, pl. 1, fig. 2; pl. 2, fig. 2.
1990 *Eoheteroceras uhligi* (Vašíček); Vašíček, pl. 1, fig. 7.

Holotype. GBAW 3932, Lower(?) Barremian, Górki Wielkie (not Jaworze, cf. Vašíček 1981, p. 123), Poland; figured by Uhlig (1883, pl. 32, fig. 10).

Other material. VŠB OT 5/30, Pi 1/6, OSM B 13 036; all crushed specimens; Lower Barremian; Outer Carpathians of the Czech Republic; GPIT 1719/10, Upper Barremian of Breggia, Southern Alps.

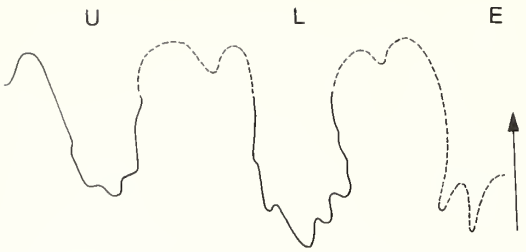
Diagnosis. Small ancylocones with involute juvenile trochospiral stage, short proversum and final hook. Strong and simple ribs are slightly prorsiradiate; interspaces become wider on retroversum.

Remarks. This species shows the typical shell morphology of *Eoheteroceras*. The initial coil is, however, more involute than in the species described above, resembling therefore the younger *Heteroceras*.

Occurrence. Lower Barremian of Ostravice, Trojanovice and Górki Wielkie, Outer Western Carpathians of the Czech Republic and Poland; Upper Barremian of Breggia Gorge, Ticino, Switzerland.

Eoheteroceras? *multicostatum* (Stahlecker, 1935)

1935 *Heteroceras multicostatum* Stahlecker, p. 282, pl. 13, figs 10–11.



TEXT-FIG. 6. Fragmentary suture-line of *Manoloviceras saharievae* (Manolov) at H = 4·5 mm (after Vašíček 1972, fig. 19).

Lectotype (designated herein). GPIT 493/13/10; Lower(?) Barremian; Maio, Cape Verde Islands; figured by Stahlecker (1935, pl. 13, fig. 10).

Revised diagnosis. Middle-sized species with elliptically criocone juvenile coil becoming arch-like with age, and then overlapping the juvenile spiral portion. Final hook unknown. Ribbing strong and simple.

Remarks. This species exhibits a certain degree of variation as shown by Stahlecker (1935). The open juvenile trochospiral stage shows it to be more similar to *Eoheteroceras* gen. nov. than to *Heteroceras*.

Occurrence. Lower(?) Barremian of Maio, Cape Verde Islands.

Genus MANOLOVICERAS gen. nov.

Type species. Hemibaculites saharievae Manolov, 1962; Lower Barremian; Kraptshene, Bulgaria.

Diagnosis. Small forms with low and open-whorled trochospiral initial coil becoming arch-like in the adult. Ribbing fine at first, later on more accentuated. Suture-line simple.

Description. The initial coil of *Manoloviceras* gen. nov. forms an open low-angle trochospiral stage. Later on, the shell becomes arch-like without forming a final hook. The juvenile shell is covered with fine and dense ribs which become stronger with age. Suture-line is of leptoceratoid type with simple outlines.

Remarks. By comparison with this monospecific genus, the suture-line in *Veleziceras* is even more simplified. *Hemibaculites* Hyatt is large, has a more complicated suture-line, and the shell closes up with a final hook, which is also the case in *Eoheteroceras* gen. nov.

Distribution. Lower Barremian of Bulgaria, Hungary and the Czech Republic.

Manoloviceras saharievae (Manolov, 1962)

Plate 4, figure 8; Text-figure 6

1883 *Hamites* (*Anisoceras*) aff. *obliquatum* d'Orbigny; Uhlig, p. 220.
1962 *Hemibaculites saharievae* Manolov, p. 536, pl. 73, figs 4–5, ?6.
1972 *Veleziceras uhligi* Vašíček, p. 56, pl. 6, figs 1–2, text-figs 17–19.
1990 *Eoheteroceras saharievae* (Manolov); Vašíček, pl. 1, fig. 5, pl. 2, figs 3, ?5.

Holotype. SGM Su Cr_1, 34; Lower Barremian; Kraptshene, Prebalkan, Bulgaria; figured by Manolov (1962, pl. 73, figs 4–5).

Other material. OSM B 13 034, 13 039, 13 041, VŠB OT 5/9, Pi 2/3, T 5/106, 267, 322; Outer Carpathians; Czech Republic; one specimen, HNM Nagy collection, Gerecse Mts, Hungary.

Revised diagnosis. Initial coil indistinctly trochospiral, later on uncoiling in a simple curved arm without final hook. Simple prorsiradiate ribs; ribs and interspaces covered with fine growth-lines. Near the mouth, ribbing is totally replaced by these growth-lines. Suture-line (Text-fig. 6) simple, with bipartite saddles, ceratite frilling and trifid *U*.

Remarks. Because of the uncommon uncoiling of *M. saharievae*, the species was previously included in *Hemibaculites*, *Veleziceras* or even *Eoheteroceras*. Instead, a new genus of the Leptoceratoidinae is here proposed for its reception. There is a certain similarity to the type species of *Hemibaculites* Hyatt, *H. obliquatus* (d'Orbigny, 1842, pl. 120, figs 1–4) of which neither suture-line nor initial coil are known. Yet, *Hemibaculites* is a much larger form, and the suture-line, at least of the North American representatives such as *H. mirabilis* Anderson, is much more complicated.

Occurrence. Lower Barremian of Kraptshene, Prebalkan, Bulgaria; Tichá and Shaft Frenštát 5, Pindula and Ostravice, Silesian Unit, Outer Carpathians of the Czech Republic; Mt Berzsek, Gerecse Mts, Hungary.

SYSTEMATIC AND STRATIGRAPHICAL CONCLUSIONS AND PHYLOGENY

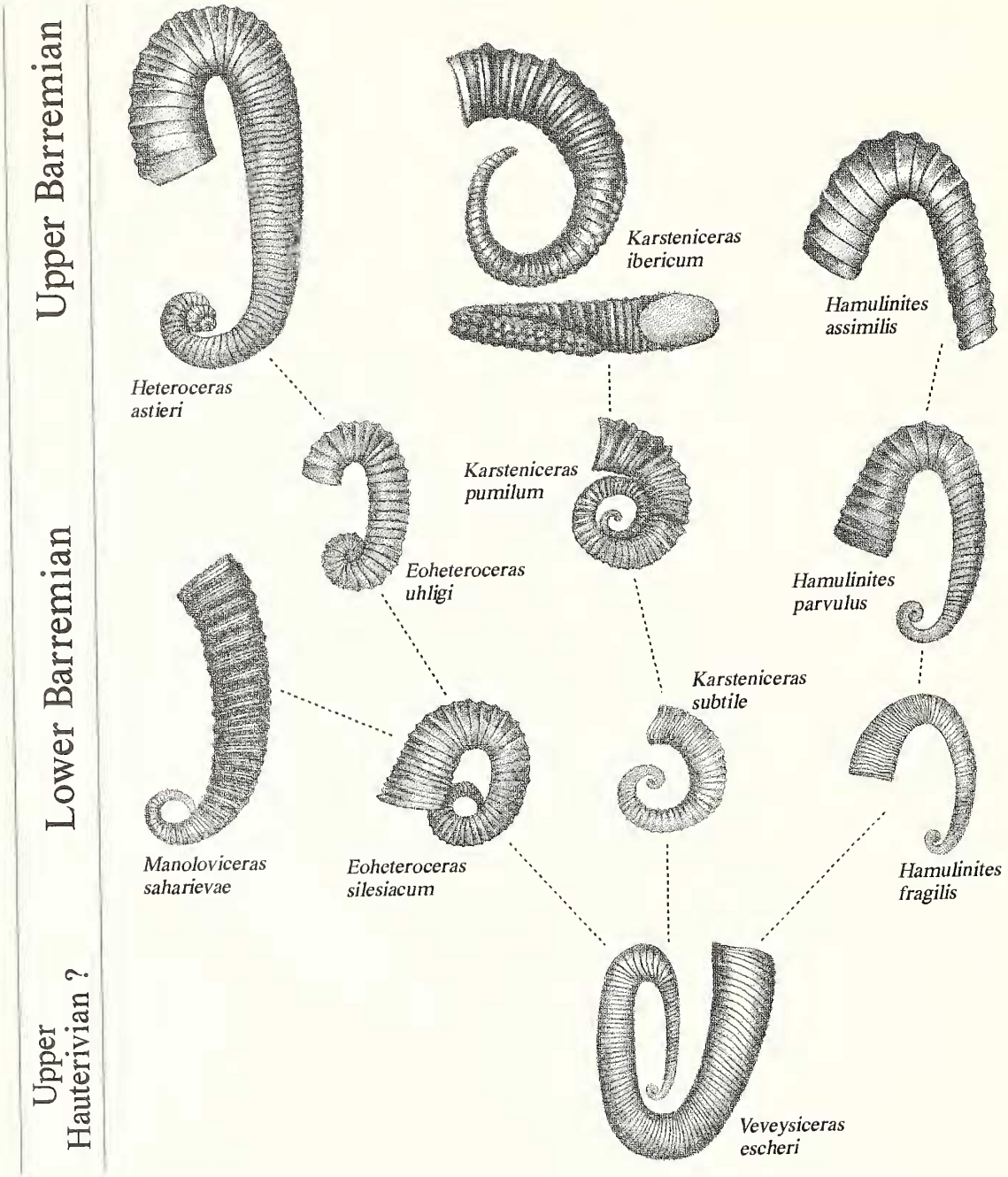
It is obvious from the systematic descriptions that the recognition of members of the Leptoceratoidinae is a difficult task. This is not only because of their small size but, above all, the reduced outline of their suture-lines. Due to the predominant occurrence of leptoceratoid species in clayey-shaly facies, preservation is, in many cases, rather poor and does not permit recognition of the suture-line. Unfortunately, this is the case with many of the holotypes of proposed species; juvenile, small-sized or fragmentary crioceratids, ancyloceratids, heteroceratids or hamulinids are in consequence not easy to separate. However, in all these groups the differentiation and denticulation of lobes and saddles is much greater at a comparable size (Wiedmann 1963; Text-fig. 9). Due to these sutural differences, some of the previously attributed 'leptoceratids' have to be excluded from this group, e.g. '*Leptoceras*' *varusense* (d'Orbigny), '*L.*' *cirtae* (Coquand) and '*L.*' *puzosianum* (d'Orbigny).

The combination of two prime characteristics (suture simplification and small size) suggests that criocones, ancylocones, hamulinicones as well as hamiticones and even heteroceraticones should be grouped in the same subfamily, Leptoceratoidinae, within the family Ancyloceratidae.

It can be seen from Text-figure 7 that, for stratigraphical reasons, *Veveysiceras* gen. nov. may represent the source of this subfamily spreading in three divergent directions. *Veveysiceras* is known from the External Prealps of Switzerland (Ooster 1860), from the Vocontian Trough and the Krížna Nappe of the Western Carpathians of Slovakia. Here *Veveysiceras* is found immediately above the beds with *Pseudothurmannia* which implies an early Lower Barremian age. A first occurrence within the Hauterivian together with *Pseudothurmannia* is assumed.

In the Krížna Nappe of the Western Carpathians the first members of *Hamulinites* co-occur with *Veveysiceras*. *Hamulinites*, representing the first evolutionary line in the Leptoceratoidinae (Text-fig. 7), becomes abundant and widespread in the middle and upper part of the Lower Barremian. While the small-sized *H. fragilis* is rare and geographically restricted (External Prealpes, Western Carpathians), *H. parvulus* is abundant and cosmopolitan during the Lower Barremian. *H. assimilis* is considered to be the last member of this genus, known only from the lower Upper Barremian of the Outer Carpathians.

Veleziceras Royo y Gómez is one of the rather poorly known representatives of this subfamily.



TEXT-FIG. 7. Evolution of Barremian Leptoceratoidinae.

The type species, *V. orbignyi*, is known from Colombia, while a second species, *V. hennigi* Stahlecker, was described from Maio, Cape Verde Islands. Both species are considered to be Lower Barremian. The origin of *Veleziceras* remains uncertain.

Karsteniceras constitutes the central stock of the subfamily. It comprises the most diverse and the longest ranging group of forms and is defined by its weakly trochospiral and criocone uncoiling. *Karsteniceras* appears with *K. subtile* and *K. pumilum* in the early Lower Barremian of Europe. Endemic regional offshoots are widespread during the Lower Barremian, i.e. the Japanese *K. asiaticum* and *K. obatai*, the Caribbean *K. trinidadense* and *K. polieri*, and the Cape Verdean *K.? filicostatum*. In the upper Lower and lower Upper Barremian a number of species develop marginal tubercles (*K. beyrichi*, *K. beyrichioide*, *K. ibericum*, *K. holzeneggeri*) or a different type of ribbing on the living chamber. These species are more widespread than the above-mentioned species and may define a number of subprovinces.

Another evolutionary line evolves from *Veveysiceras* towards *Eoheteroceras* and *Manoloviceras*. *Eoheteroceras* represents the 'type' of this evolutionary line and to some extent foreshadows the later genus *Heteroceras*. It is long-ranging, starting in the early Lower Barremian with the Carpathian species *E. silesiacum*; including in the Lower Barremian the endemic *E. norteyi* (from Cuba) and *E.? multicostatum* (from the Cape Verde Islands); and ending up with *E. uhligi*, which is known from the late Lower Barremian of the Outer Carpathians and early Upper Barremian of Ticino, Southern Alps. Increasing size seems to be a general trend in each of the three separate evolutionary lines. *Manoloviceras*, however, is considered to be a lateral offshoot loosing the final hook. It is regionally rather restricted and of Lower Barremian age.

Text-figure 8 gives an idea of suture-line constancy and variation in leptoceratids. At first glance, suture-lines of the main representatives of this group look very similar with regard to their simplification in the adult stage. However, the three evolutionary lines defined above (Text-fig. 7) can be recognized by specific lobe or saddle differentiation. While in *Hamulinites* saddles tend to be more frilled, in *Manoloviceras* the frilling of lobes increases. The cryptogenous *Veleziceras* exhibits the most simplified adult suture-line (Text-fig. 9).

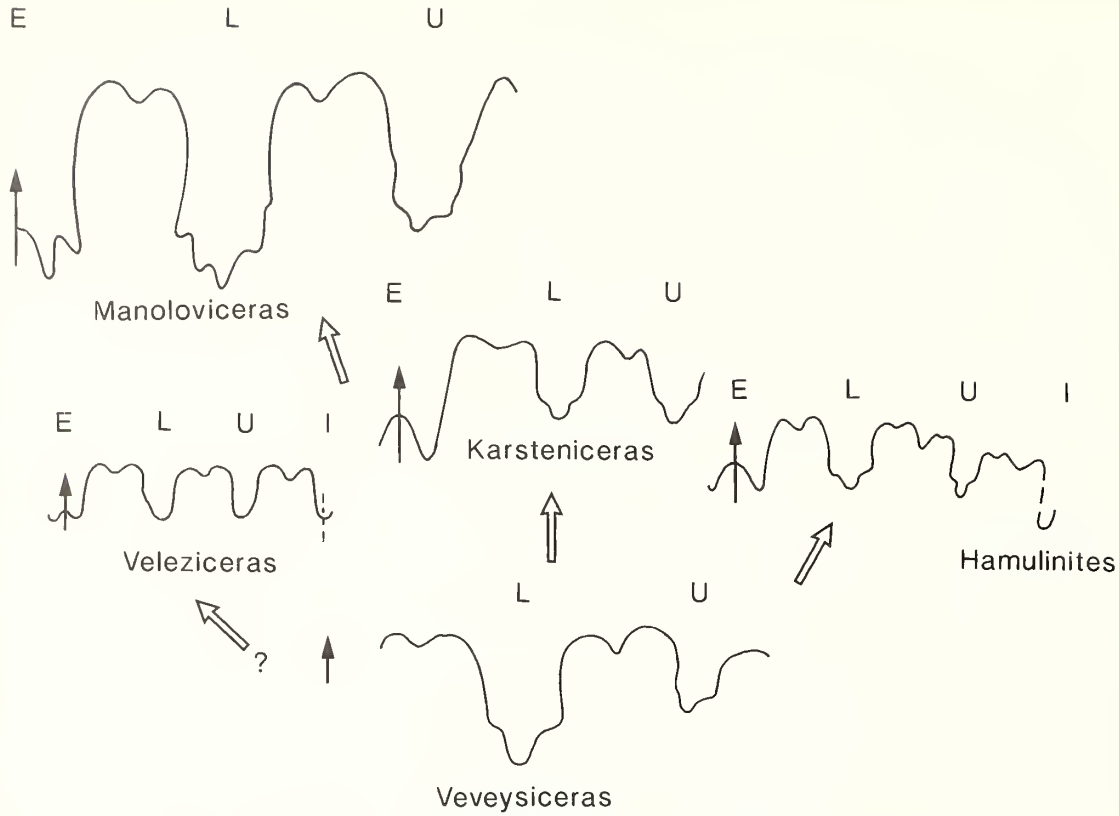
While we can assume that the evolutionary line *Veveysiceras–Eoheteroceras* leads to the large-sized *Heteroceras* d'Orbigny near the Lower/Upper Barremian boundary, we have no idea yet about the ancestor of either *Veveysiceras* or the Leptoceratoidinae. These forms are certainly unrelated to the homoeomorphic true leptoceratids of Berriasian to Valanginian age.

PALAEOGEOGRAPHY

Text-figures 10 and 11 give the regional distribution of leptoceratoids. The Leptoceratoidinae have their main distribution on the southern shelf margin of the European Plate, from the Caucasian Basin in the east, to the Prebetic and Subbetic Basins in southern Spain in the west.

Akopyan (1962) described *Karsteniceras* cf. *pumilum* from the Zangezur Mts, Armenian Caucasus (Kafan area of Kotetishvili 1989). Favoured areas for leptoceratoids were the Bulgarian Prebalkan and the southern and western margins of the Moesian Platform. From Bulgaria, Lower Barremian *Hamulinites*, *Karsteniceras* and *Manoloviceras* were recorded by Manolov (1962), Breskovski (1966), Dimitrova (1967) and Nikolov (1987), from a well oxidized marly facies. Avram (1988) summarized the Romanian occurrences. Here, all the Bulgarian genera were also recorded from the western Moesian Platform margin, e.g. mainly from pelagic facies at Sviniţa, Marginal Dacides. From flysch deposits of the Outer Dacidic Nappes, *Hamulinites* and *Karsteniceras* were reported, while from the pelagic facies in the Getic Nappe (Median Dacides) only the genus *Karsteniceras* is known.

Another evolutionary centre for leptoceratoids during Lower Barremian (and lower Upper Barremian) time was the Silesian Nappe in the Outer Western Carpathians of the Czech Republic and Poland (Vašíček 1972, 1981, 1990). In dark-grey flyschoid clays, ten species can be detected which belong to *Karsteniceras*, *Hamulinites*, *Eoheteroceras* and *Manoloviceras* in descending order.



TEXT-FIG. 8. Evolutionary trends in adult suture-lines of the Leptoceratoidinae.

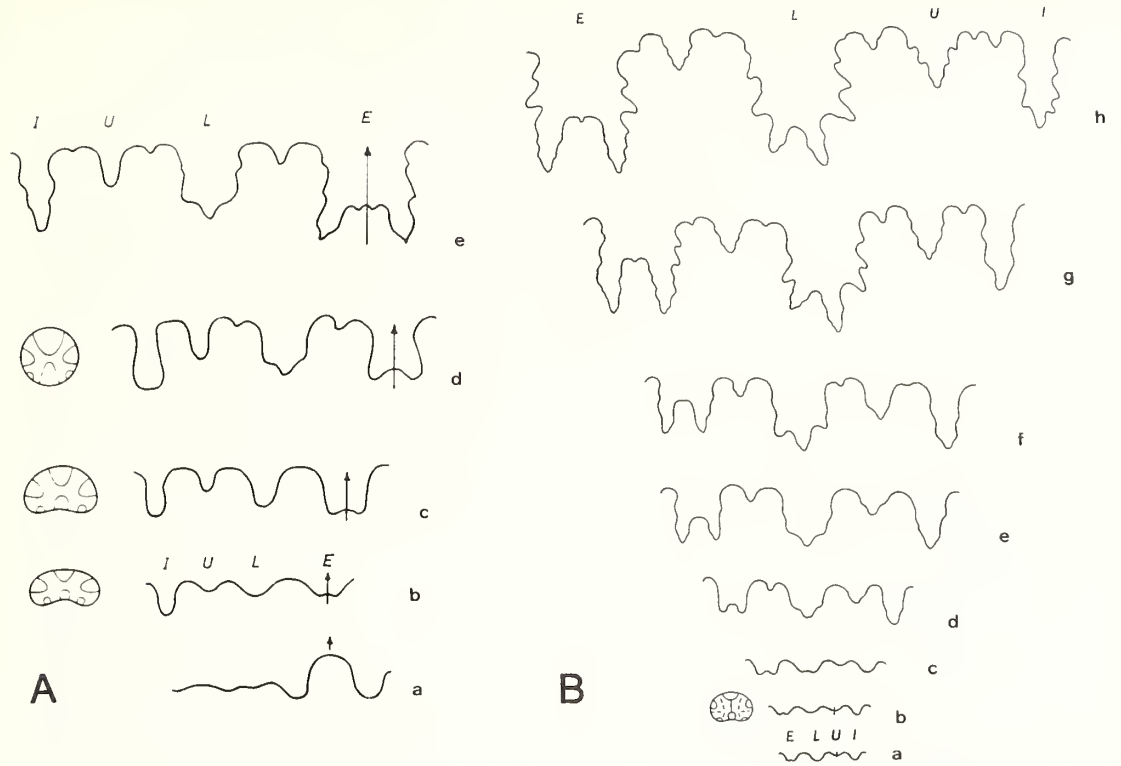
The next occurrences further west are the Austrian Helvetic Drusberg Marls with *Karsteniceras* (Wiedmann 1977), and the dark-grey marls of the External Prealps (Vaud, Switzerland). In Switzerland, nearly the same diversity as in the Carpathians was detected by Ooster (1860) and Sarasin and Schöndelmeyer (1902). The Swiss leptoceratoids are here referred to the genera *Karsteniceras*, *Hamulinites* and *Veveysiceras*.

From the southern margin of the Vocontian Trough, southeastern France, *Veveysiceras* and *Hamulinites* are newly described from light-grey Lower Barremian marls. The westernmost occurrences in the European Tethyan Realm are reported in light-grey Lower Barremian marls from the Prebetic Platform and the Subbetic Trough in southern Spain.

Leptoceratoidinae occur less abundantly on the northern margin of the African Plate. *Karsteniceras* and *Eoheteroceras* are recognized (Rieber 1977; this paper) in Lower–Upper Barremian dark intercalated shales in the upper Maiolica in Ticino, Southern Alps. *Karsteniceras* and *Hamulinites* occur in a light-grey marly facies in the Lower Barremian Rossfeld Beds of the Austroalpine Alps.

An easternmost occurrence, light-grey slope marls of the Krížna Nappe, Central Western Carpathians of Slovakia, has yielded *Veveysiceras*, *Karsteniceras* and *Hamulinites* (Borza *et al.* 1984; this paper).

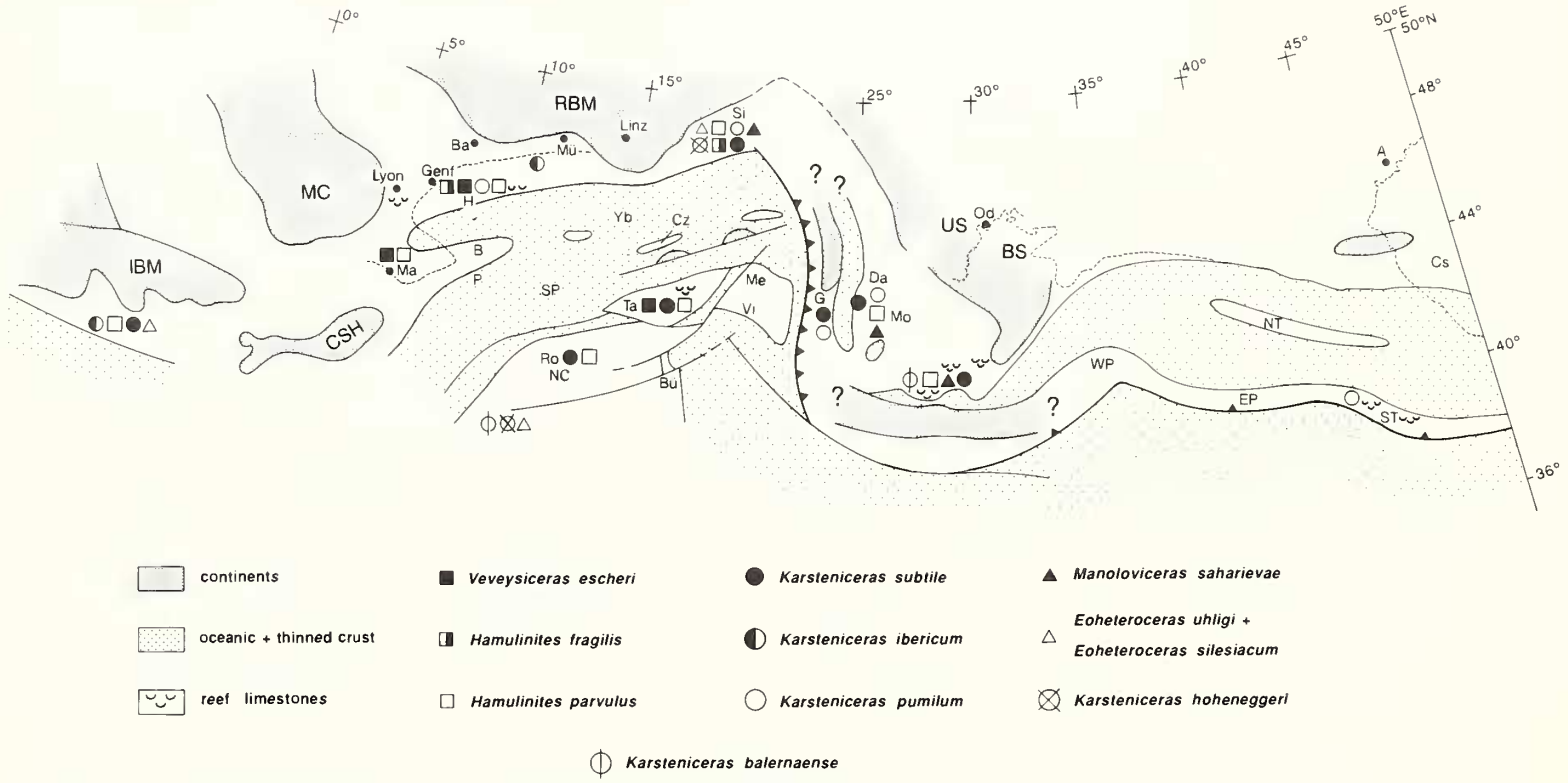
Considering the global distribution of the Leptoceratoidinae (Text-fig. 10), the supposed occurrences in northern Africa cannot be confirmed, i.e. '*Leptoceras*' *cirtae* Coquand, 1880 from Algeria, and the '*Leptoceras*' *puzosianum* (d'Orbigny) of Burrolet *et al.* (1983) from Tunisia.



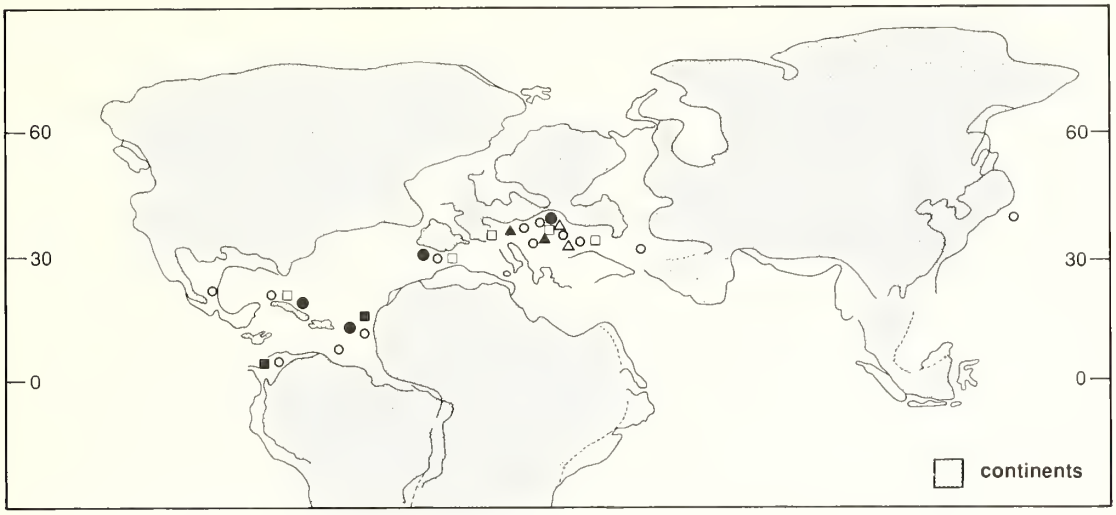
TEXT-FIG. 9. Comparison of suture ontogenies in leptoceratoids. A, *Hamulinites parvulus* (Uhlig) [= *H. munieri* (Nicklès)], GPIT 1247/2; Lower Barremian; La Querola, Cocentaina, Spain; a, prosuture; b, primary suture and septal surface; c, at WH 0·5 mm; d, intermediate stage; e, at WH 2·5 mm (from Wiedmann 1963). B, *Leptoceras studeri* (Ooster), GPIT 1372/2; Berriasian; Rufisgraben-Jusital, Switzerland; a, primary suture; b, tenth suture and septal surface; c, 13th suture; d, 20th suture at WH 1·5 mm; e, intermediate stages; h, adult suture at WH 3·5 mm (from Wiedmann 1969).

The equatorial–subequatorial Atlantic was, however, another area favoured by leptoceratoids. In the SE North Atlantic, Stahlecker (1935) discovered representatives of the genera *Karsteniceras*, *Veleziceras* and *Eoheteroceras* in platy basinal Lower Barremian limestones from Maio, Cape Verde Islands. Another centre of occurrence is the Caribbean. Here, we know *Karsteniceras* from Trinidad (Imlay 1954) and *Hamulinites* and *Eoheteroceras* in micritic limestones of the Polier Formation of Cuba (Myczyński 1977; Myczyński and Triff 1986). *Karsteniceras* is described from the Lower Barremian Santuario Formation in Querétaro, México, (González-Arreola and Carillo-Martínez 1986), while the black nodular Lower Barremian limestones of the Sabana de Bogotá, Colombia, contain *Karsteniceras* and *Veleziceras* (Karsten 1858; Royo y Gómez 1945; Etayo Serna 1968). Recent investigations in the Japanese Lower Cretaceous by Matsukawa (1987, 1988) have added the western Pacific to the distributional range. *Karsteniceras* was recorded from the clayey-sandy Ishido Formation and concretions in the Kimigahama Formation, both in the Lower Barremian of Hondo.

The spreading and evolutionary centre of the Leptoceratoidinae was thus the northern margin of the western and central Tethys (Text-fig. 11). Especially on the southern shelf of the central European Plate leptoceratoids prospered in basinal environments with a dominance of clayey-marly facies. From this evolutionary centre, they presumably followed the North Equatorial Current in



TEXT-FIG. 10. Distribution of Barremian Leptoceratoidinae in Europe. Endemic species are not considered. Palaeogeography adopted from Dercourt *et al.* (1985, 1990). Abbreviations: B, Briançonnais; BS, Black Sea; Bü, Bükk, Cs, Caspian Sea; CSH, Cor-Sardinian High; Cz, Czorsztyn; Da, Danubian; EP, Eastern Pontides; G, Getic; H, Helvetic; IBM, Iberian Meseta; MC, Central Massif; Me, Mecsek; Mo, Moesia; NC, Northern Calcareous Alps; NT, Northern Transcaucasus; P, Piemontais; RBM, Rhenish-Bohemian Massif; Ro, Rossfeld; Si, Silesian; Sp, South Penninic; ST, Southern Transcaucasus; Ta, Tatric; US, Ukrainian Shield; Vi, Villány; WP, Western Pontides; Yb, Ibbsitz.



TEXT-FIG. 11. Global distribution of Leptoceratoidinae; Barremian palaeogeography after Barron (1987).

a westward direction (see also Gordon 1973; Klinger *et al.* 1984; Obata and Matsukawa 1988; Klinger 1990) to colonize the Atlantic and Pacific oceans.

PALAEOECOLOGY

Leptoceratoid palaeoecology is highly speculative but can be inferred using the following data.

Leptoceratoids are to some extent global in distribution, but have an interesting E–W gradient ranging from the evolutionary centre in central and southeastern Europe to Japan. In the western Tethys they are practically restricted to the northern oceanic margin. The favoured sedimentary facies are clayey and limey marls. These marls are either dark-grey to black with increasing contents of organic matter and pyrite, or light-grey and well-oxygenated. Leptoceratoids also occur in flysch and flysch-like deposits.

Leptoceratoidinae show variation in shell size, shell form, mode of uncoiling, strength and density of ribbing, and in the otherwise very stable form of the external lobe *E.* This may be related to a more or less distinct shell torsion in some of the genera.

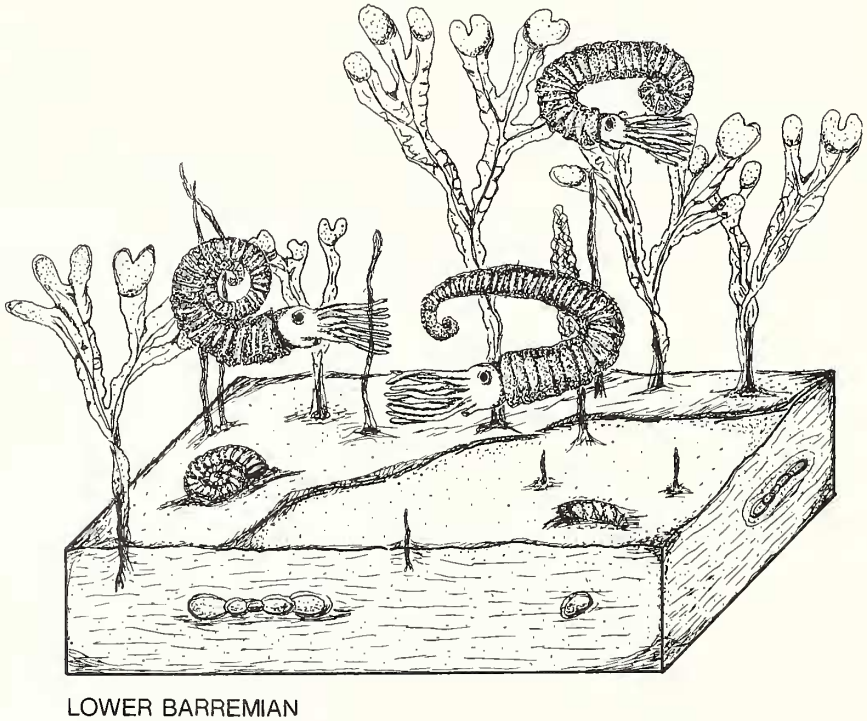
The only discussion of life habit available is given by Rieber (1977), who described *Karsteniceras balernaense* from Breggia. He concluded that this species led a nektonic existence in the oxygenated Tethyan Ocean above anoxic bottom conditions. These conditions were inferred from the black marly sediment enriched in organic matter and pyrite, and from the absence of definite benthos.

Westermann (1990), in a stimulating paper on ammonite depth distributions, located the criocone heteromorphs in shallow marine habitats of the inner shelf.

One of the most abundant occurrences of leptoceratoids is in the dark-grey marls of the Těšín-Hradiště Formation (formerly Wernsdorfer Beds) of the Silesian Unit, Outer Carpathians (Uhlig 1883; Vašíček 1977). These beds (and most probably their organic content too) are, however, of turbiditic origin. Leptoceratoids have not only their maximum diversity, but also their maximum density within these beds, where they sometimes occur concentrated in 'nests' (Pl. 4, fig. 8). These maxima are generally found in the autochthonous layers between two turbidites. Perfect preservation, especially of the fragile initial coil and the co-occurrence of two-valved inoceramids

(Pl. 2, fig. 6), supports the idea that shells were not transported but were deposited close to the original biotope. It is true, however, that the total faunal 'association' is diverse and includes phylloceratids and lytoceratids as well as heteroceratids and true Ammonitina. This association is considered to be a representative cross-section through the whole water column.

These observations have much in common with those of Dietl (1973, 1978) who described Middle Jurassic spiroceratids having their maximum distribution in the Suebian basinal facies with stagnant conditions. Spiroceratid abundance decreases towards the more oxygenated oolitic shallow water realm. Dietl (1978, p. 70) inferred a bottom-related, vagrant life habit for spiroceratids which preferred to live in algal mats. The similar depositional environment and shell morphology (partial torsion) of spiroceratids and leptoceratoids support the idea of a similar life habit (Text-fig. 12).



TEXT-FIG. 12. Model of leptoceratoid life habit.

From their geographical distribution an E–W gradient can be observed, while the Tethyan Ocean was an obvious barrier for N–S crossing. Transportation by the E–W running North Equatorial Current is unlikely for benthic animals. As most cephalopods favour nearshore breeding places, leptoceratoids may have been prone to drifting in surface currents during their early juvenile stages. For these tiny and fragile forms, however, a planktonic mode of life cannot be totally refuted.

Acknowledgements. Both authors are much indebted to the Alexander von Humboldt Foundation for facilitating this collaboration, to W. Wetzel, K. Mezihoráková, M. Grmelová and D. Korn for the good quality of the photographs, to Dr F. Etayo Serna (Bogota), Dr W. Kuhnt (Tübingen) and J. Manthey (Tübingen) for contributing additional specimens, and to Dr D. Decrouez (Genève), Dr H. Immel (München), Dr I. Z. Nagy (Budapest), Dr G. Schairer (München), Dr H. A. Stalder (Bern) and Dr F. Stojaspal (Wien)

for making available specimens and casts from their collections. Some of the figures were kindly prepared by H. Vollmer and R. Schoch (Tübingen). The authors appreciate the valuable comments of the reviewers.

REFERENCES

AKOPYAN, V. T. 1962. *Stratigrafiya yurskikh i myelovykh otlosheniy yugo-vostotshnovo Zangezura.* Izdatyelstvo Akademiya Nauk Armyanskoi SSR, Erevan, 265 pp. [In Russian].

ASTIER, J. E. 1851. Catalogue des *Ancyloceras* appartenant à l'étage néocomien d'Escragnolles et des Basses-Alpes. *Annales des Sciences Physiques et Naturelles, d'Agriculture et de l'Industrie*, 2ème série, **3**, 435–456.

AVRAM, E. 1976. La succession des dépôts Tithoniques supérieurs et Crétacés inférieurs de la région de Sviniţa (Banat). *Dări Seamă ale Şedinţelor*, **62**, 53–71.

—— 1988. The early Cretaceous (Berriasian–Barremian) ammonite assemblages in Roumania, 607–619. *In* WIEDMANN, J. and KULLMANN, J. (eds). *Cephalopods – present and past.* Schweizerbart, Stuttgart, xiii + 765 pp.

—— and KUSKO, M. 1984: Céphalopodes éocrétacés de la partie centrale et méridionale des monts Baraolt (Carpathes orientales). *Dări Seamă ale Şedinţelor*, **79**, 5–24.

BARRON, E. J. 1987. Global Cretaceous paleogeography – International Geologic Correlation Program Project 191. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **59**, 207–214.

BORZA, K., MICHALÍK, J., GAŠPARÍKOVÁ, V. and VAŠÍČEK, Z. 1984. The biostratigraphy of the Hauterivian/Barremian boundary beds in the Krížna Nappe, Western Carpathian (Czechoslovakia). *Cretaceous Research*, **5**, 349–356.

BRESKOVSKI, S. 1966. Biostratigraphie du Barrémian au sud du village de Brestak, dans la région de Varna. *Travaux sur la Géologie de Bulgarie*, **8**, 71–112.

BUROLLET, P. F., MEMMI, L. and M'RABET, A. 1983. Le Crétacé inférieur de Tunisie. Aperçu stratigraphique et sédimentologique. *Zitteliana*, **10**, 255–264.

COQUAND, H. 1880. Etudes supplémentaires sur la paléontologie algérienne, faisant suite à la description géologique de la région sud de la province de Constantine. *Bulletin de l'Académie Hippone*, **15**, 1–449.

COTTREAU, J. 1937. Types du Prodrome de Paléontologie stratigraphique universelle de D'Orbigny. Tome III (Néocomien). Part 3. *Annales de Paléontologie*, **26**, 53–84.

DARGA, R. and WEIDICH, K. F. 1986. Die Lackbach-Schichten, eine klatische Unterkreide-Serie in der Unkener Mulde (Nördliche Kalkalpen, Tirolikum). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie*, **26**, 93–109.

DERCOURT, J., and 16 others. 1985. Présentation de 9 cartes paléogéographiques au 1/20.000.000e s'étendant de l'Atlantique au Pamir pour la période du Lias à l'Actuel. *Bulletin de la Société Géologique de France*, 8ème série, **1**, 637–652, 10 pls.

—— RICOU, L. E., ADAMIA, S., CZASZAR, G., FUNK, H., LEFELD, J., RAKÚS, M., SĂNDULESCU, M., TOLLMANN, A. and TCHOUMACHENKO, P. 1990. Anisian to Oligocene paleogeography of the European margin of Tethys (Geneva to Baku). 159–190, 11 maps. *In* RAKÚS, M., DERCOURT, J. and NAIRN, A. E. M. (eds). Evolution of the northern margin of Tethys: The results of IGCP Project 198. Volume 3. *Mémoires de la Société Géologique de France*, **154** (3), 1–220, 11 maps.

DIETL, G. 1973. Middle Jurassic (Dogger) heteromorph ammonites. 283–285. *In* HALLAM, A. (ed.). *Atlas of palaeobiogeography.* Elsevier, Amsterdam, xii + 531 pp.

—— 1978. Die heteromorphen Ammoniten des Dogger (Stratigraphie, Taxonomie, Phylogenie, Ökologie). *Stuttgarter Beiträge für Naturkunde*, **33**, 1–76.

DIMITROVA, N. 1967. *Les fossiles de Bulgarie. IV. Crétacé inférieur. Cephalopoda (Nautiloidea et Ammonoidea).* Académie Bulgare des Sciences, Sofia, 236 pp. [In Bulgarian with French summary].

—— 1970. Phylogenèse des Ammonites hétéromorphes du Crétacé inférieur. *Izvestiya na Geologitsheskaya Institut, Seriya palaeontologiya*, **19**, 71–110.

DRUSHTCHIC, V. V. 1960. [Ammonites Part 1]. 249–308. *In* DRUSHTCHIC, V. V. and KUDRYAVTSEV, M. P. (eds). *Atlas nishnemyelovoy fauny severnovo Kavkaza i Kryma.* Gostoptekhyzdat, Moscow, 396 pp. [In Russian].

ETAYO SERNA, F. 1968. Apuntaciones acerca de algunas amonitas interesantes del Hauteriviano y del Barremiano de la región de Villa de Leiva (Boyacá, Colombia, S.A.). *Boletin Geológico de la Universidad de Santander*, **24**, 51–70.

GÉRARD, C. and CONTAUT, H. 1936. Les ammonites de la zone à Peltoceras athleta du Centre-Ouest de la France. *Mémoires de la Société géologique de France*, Nouvelle Série, **13**, mémoire 29, 79 pp.

GILL, T. 1871. Arrangement of the families of mollusks. *Smithsonian Miscellaneous Collections*, **227**, i–xvi + 1–49.

GONZÁLEZ-ARREOLA, C. and CARILLO-MARTÍNEZ, M. 1987. Amonitas del Jurásico superior (Titoniano superior) y del Cretácico inferior (Hauteriviano–Barremiano) del área de San Joaquín-Vizarrón, Estado de Querétaro. *Universidad National Autónoma de México, Instituto de Geología, Revista*, **6** (2), 171–177.

GORDON, W. A. 1973. Marine life and ocean surface currents in the Cretaceous. *Journal of Geology*, **81**, 269–284.

IMLAY, R. W. 1954. Barremian ammonites from Trinidad, B.W.I. *Journal of Paleontology*, **28**, 662–667.

IMMEL, H. 1987. Die Kreideammoniten der nördlichen Kalkalpen. *Zitteliana*, **15**, 3–163.

KARSTEN, H. 1858. Über die geognostischen Verhältnisse des westlichen Columbien, der heutigen Republiken Neu-Granada und Equator. *Amtliche Berichte*, **32**, *Versammlung Deutscher Naturforscher und Ärzte*, 80–117.

KILIAN, W. 1907–1913. Unterkreide (Palaeocretacium). 398 pp. *In* FRECH, F. (ed.) *Lethaea geognostica. II. Mesozoikum, Volume 3. Kreide*. Schweizerbart, Stuttgart.

KLINGER, H. C. 1990. Upper Barremian Heteroceratinae (Ammonoidea) from the Caucasus, Zululand and Patagonia: palaeobiogeographic significance. *Cretaceous Research* **11**, 321–329.

—— KAKABADZE, M. V. and KENNEDY, W. J. 1984. Upper Barremian (Cretaceous) heteroceratid ammonites from South Africa and the Caucasus and their paleobiogeographic significance. *Journal of Molluscan Studies*, **50**, 43–60.

KOTETISHVILI, E. V. 1989. Biofacies characteristics of Lower Cretaceous deposits of Georgia. 543–550. *In* WIEDMANN, J. (ed.). *Cretaceous of the Western Tethys*. Schweizerbart, Stuttgart, xiv + 1005 pp.

KULLMANN, J. and WIEDMANN, J. 1970. Significance of sutures in phylogeny of Ammonoidea. *University of Kansas Palaeontological Contribution*, **47**, 1–32.

LUPPOV, N. P. and DRUSHTCHIC, V. V. 1958. Mollyuski – Golovonogiye. II. Ammonoidei (Cerati ty i Ammonity). Vnutrennerakovinnye. Prilozheniye: Konikonkhii. *Osnovy Paleontologii*. Gosudarstvennoye N.T. Izdatyelstvo, Moscow, 190 pp. [In Russian].

MANOLOV, J. R. 1962. New ammonites from the Barremian of North Bulgaria. *Palaeontology*, **5**, 527–539.

MANTHEY, J. 1991. Stratigraphische und fazielle Untersuchungen im westlichen Subbetikum (Sierra de las Cabras, Sierra de la Sal und Sierra del Valle, Provincia de Cádiz, Süd-Spanien). Unpublished Diplome Thesis, Universität Tübingen.

MATSUKAWA, M. 1987. Early shell morphology of *Karsteniceras* (ancyloceratid) from the Lower Cretaceous Choshi Group, Japan and its significance to the phylogeny of Cretaceous heteromorph ammonites. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, **148**, 346–359.

—— 1988. Barremian ammonites from the Ishido Formation, Japan – supplements and faunal analysis. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, **149**, 396–416.

MYCZYŃSKI, R. 1977. Lower Cretaceous ammonites from Sierra del Rosario (Western Cuba). *Acta Palaeontologica Polonica*, **22**, 139–173.

—— and TRIFF, J. 1986. Los ammonites del Cretácico Inferior de las provincias de Pinar del Río y Matanzas. *Bulletin of the Polish Academy of Sciences, Earth Sciences*, **34**, 113–137.

NAGY, I. Z. 1967. Unterkretazische Cephalopoden aus dem Gerecse-Gebirge. *Annales Historico-Naturales Musei Nationalis Hungarici, pars Mineralogica et Geologica*, **59**, 53–73.

NICKLÈS, R. 1894. Contributions à la paléontologie du Sud-Est de l'Espagne. Terrain Crétacé. Néocomien (suite). *Mémoires de la Société Géologique de France*, **4** (Mémoire 4), 31–59.

NIKOLOV, T. 1967. *Protoleptoceras* gen. n. – a new genus of Berriassian ammonites. *Comptes Rendus de l'Académie Bulgare des Sciences*, **19** (9), 839–841.

OBATA, I. and MATSUKAWA, M. 1988. Some boreal or subboreal ammonites in the Japanese Barremian. 469–476. *In* WIEDMANN, J. and KULLMANN, J. (eds). *Cephalopods – present and past*. Schweizerbart, Stuttgart, xiii + 765 pp.

OOSTER, W. A. 1860. Catalogue des Céphalopodes fossiles des Alpes suisses. IV. Partie: Céphalopodes tentaculifères, Ammonitides, G. *Ammonites. Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft der Gesamten Naturwissenschaften*, **18**, 160 pp.

ORBIGNY, A. D'. 1840–1842. Terrains crétacés. I. Céphalopodes. *Paléontologie française*. Masson, Paris, 662 pp.

—— 1850. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés. Corallien-Crétacé-Parisien*, **2**. Masson, Paris, 427 pp.

—— 1852. Notice sur le genre *Hamulina*. *Journal de Conchyliologie*, **3**, 207–228.

PAQUIER, V. 1900–1901. Recherches géologiques dans le Diois et les Baronnies orientales. *Annales de l'Université de Grenoble*, **12**, 373–516 + appendix.

PICTET, F.-J. and LORIOL, P. DE 1858. Description des fossiles contenu dans le terrain Néocomien de Voirons, Description des animaux invertébrés. *Matériaux de la Paléontologie Suisse*, **2** (1), 1–64.

RIEBER, H. 1977. Eine Ammonitenfauna aus der oberen Maiolica der Breggia-Schlucht (Tessin, Schweiz). *Eclogae geologiae Helvetiae*, **70**, 777–787.

ROMAN, F. 1938. *Les ammonites Jurassiques et Crétacées. Essai de Genera*. Masson, Paris, 554 pp.
ROYO Y GÓMEZ, J. 1945. Fósiles del Barremiense colombiano. *Compilaciones de estudios geológicos oficiales de Colombia*, **6**, 455–495.
SARASIN, CH. and SCHÖNDELMAYER, C. 1902. Étude monographique des ammonites du Crétacique inférieur de Châtel-Saint-Denis. *Mémoires de la Société Paléontologique Suisse*, **28/29**, 195 pp.
SARKAR, S. 1954. Some new genera of uncoiled ammonites from Lower Cretaceous. *Science and Culture*, **19** (12), 618–620.
—— 1955. Revision des ammonites déroulées du Crétacé inférieur du Sud-Est de la France. *Mémoires de la Société Géologique de France, Nouvelle Série*, **72**, 176 pp.
SAYN, G. 1891. Description des ammonites du Barrémian du Djebel-Ouach (près Constantine). *Annales de la Société d'Agriculture*, 6ème série, **3**, 135–208.
STAHLECKER, R. 1935. Neocom auf der Kapverden-Insel Maio. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **1934**, 265–301.
THIEULOY, J.-P. 1966. Leptocères berriasiens du massif de la Grande-Chartreuse. *Travaux du Laboratoire de Géologie, Grenoble*, **42**, 281–295.
UHLIG, V. 1883. Die Cephalopoden der Wernsdorfer Schichten. *Denkschriften der k. k. Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse*, **46**, 127–290.
VAŠÍČEK, Z. 1972. Ammonoidea of the Těšín-Hradiště Formation (Lower Cretaceous) in the Moravskoslezké Beskydy Mts. *Rozpravy Ústředního Ústavu Geologického*, **38**, 103 pp.
—— 1981. Zwei neue faunistische Fundorte der Unterkreide in der Silesischen Einheit und Zusammenfassung der Revision der von V. Uhlig (1883) beschriebenen Ammoniten. *Sborník Vedeckých Prací Vysoké Školy Báňšské v Ostravsě*, **25** (2, for 1979), 119–133.
—— 1990. Unterkreide-Ammoniten aus neu abgeteuften Schächeten im Gebiet von Frenštát-Trojanovice (Äussere Karpaten, Silesische Einheit, ČSFR). *Acta Musei Moraviae, Scientiae Naturales*, **75**, 95–106.
WEDEKIND, R. 1916. Zur Systematik der Ammonoidea. *Centralblatt für Mineralogie*, **1916**, 529–538.
WESTERMANN, G. E. G. 1990. New developments in ecology of Jurassic–Cretaceous ammonoids. 459–478. *In* PALLINI, G., CECCA, F., CRESTA, S. and SANTANTONIO, M. (eds). *Fossili, Evoluzione, Ambiente, Atti del 2° Convegno internazionale F.E.A., Pergola 1987*. Comitato Centenario Raffaelo Piccinini, Pergola, 516 pp.
WIEDMANN, J. 1963. Entwicklungsprinzipien der Kreideammoniten. *Palaeontologische Zeitschrift*, **37**, 103–121.
—— 1969. The heteromorphs and ammonoid extinction. *Biological Reviews*, **44**, 563–602.
—— 1972. Neue Vorstellungen über Stammesgeschichte und System der Kreideammoniten. *Proceedings of the 23rd International Geological Congress, Prague 1968, International Palaeontological Union*, 93–118.
—— 1973. Ancyloceratina (Ammonoidea) at the Jurassic/Cretaceous boundary. 309–316. *In* HALLAM, A. (ed.). *Atlas of palaeobiogeography*. Elsevier, Amsterdam, xii + 531 pp.
—— 1977. On the significance of ammonite nuclei from sieve residues. *Annales des Mines et de la Géologie*, **28**, 135–161.
WRIGHT, C. W. 1957. Cretaceous ammonites. *In* ARKELL, W. J., KUMMEL, B. and WRIGHT, C. W. *Mesozoic Ammonoidea*. L80–L465. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part L. Mollusca 4. Cephalopoda–Ammonoidea*. Geological Society of America and University of Kansas Press, New York and Lawrence, Kansas, 490 pp.
—— 1981. Cretaceous Ammonoidea. 157–174. *In* HOUSE, M. R. and SENIOR, J. R. (eds). *The Ammonoidea*. Systematics Association Special Volume, **18**. Academic Press, London, xiv + 593 pp.
YABE, H., NAGAO, T. and SHIMIZU, S. 1926. Cretaceous Mollusca from the Sanchû Graben in the Kwantô Mountainland, Japan. *Science Report of the Tôhoku Imperial University, Series 2, Geology*, **9**, 33–76.

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Typescript received 1 September 1992
Revised typescript received 6 July 1993